ECOLOGY AND POPULATION DYNAMICS OF THE BLACK BULLHEAD, *ICTALURUS MELAS* (RAFINESQUE), IN CENTRAL KENTUCKY

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ABSTRACT

The black bullhead, *Ictalurus melas* (Rafinesque), is a prominent element of the fish fauna in central Kentucky, but relatively little has been reported concerning either the population dynamics or physiological ecology in that area. This work reports growth and reproduction in pond, lake and stream populations of the black bullhead. Emphasis was placed on pond populations for the analysis of reproductive development, longevity and survival. Some aspects of the physiological ecology, including temperature ranges and oxygen consumption rates, were measured as functions of prior acclimation histories.

Black bullheads were well-represented in each of the habitats surveyed; however, growth in length and in weight, expressed as a function of age at the time of annulus formation, was significantly lower for fish taken from ponds. Pond populations exhibited the ability to achieve great numbers, and the effect of crowding was significantly reflected in lower length-weight and age-weight correlations, and in lower mean fecundity. Mortality in ponds was high throughout the year, and highest during spring and early summer. Adult black bullheads sampled from all populations relied heavily on chironomid larvae as a staple source of food, although this item had a selection value comparable to several less abundant food sources. Larval feeding was found to be highly selective. Reproductive development, and the attainment of peak gonad weight-body weight ratios was retarded in ponds as compared with development in lakes and streams. Temperature thresholds measured at 7°, 12° and 23°C indicated that different life stages responded differently to temperature. Upper critical thresholds for the first four free-swimming stages formed a graded sequence, with lower thresholds graduated upward in direct proportion to upper critical values. Preference ranges differed significantly for postlarval through yearling stages. Oxygen consumption rates, Q10 values, and absolute consumption curves suggested a relative insensitivity to temperature. Black bullheads ranging in weight from 20.15 to 37.00 g had a critical oxygen consumption value per gram of 0.1 ml. O_2/g/hr at 0.2 to 0.5 ml/l ambient oxygen.

INTRODUCTION

Changes in fish stocking combinations (Swingle, 1950), shifts in angler preferences (Houser and Collins, 1962) and selective construction of commercial gear to favor larger, if less abundant, fishes have deemphasized the value of the black bullhead. Although management personnel and anglers in Kansas and Iowa (Hastings and Cross, 1962; Forney, 1955) continue to prize this species for its angling value most states east of the Mississippi River have shown little interest in bullhead propagation and management for sport or commercial purposes since early in the present century.

General disregard for the black bullhead is reflected in the early complete absence of investigations designed to foster a better understanding of its potentials and limitations. In short, very little is known concerning many important aspects of the life history and physiological ecology of *I. melas*, aspects that might prove valuable if the species is to be most effectively utilized or managed. No detailed bullhead investigations have been conducted in Kentucky waters. Reports that have appeared (Clay, 1962) have simply acknowledged the

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species' presence and recorded some of its taxonomic features.

The purpose of this study is to present pertinent aspects of the black bullhead life cycle in order to assess the species' ecological interactions, and to analyze some physiological phenomena which favor the fish in some habitats and restrict it in others. The study was begun in April 1970 and terminated in early July 1971. During this period, our investigation concentrated on the reproductive potential, natural mortality, feeding behavior and food, and physiological ecology associated with the black bullhead's success in natural and impounded waters, with particular emphasis on the earlier stages of life. However, several aspects of adult biology not previously investigated in Kentucky waters were studied with significant results.

REVIEW OF THE LITERATURE

Black bullheads have been found in virtually every type of fresh-water habitat. Houser and Collins (1962), for example, indicated that no important Oklahoma water was free of this species. Although sampled from reservoirs, lakes and streams, the only significant populations were encountered in smaller bodies of water. This finding is supported by the results of lake and stream investigations conducted throughout the range (Lynch, Buscemi and Lemmons, 1951; Trautman, 1957). According to Fogel (1964), black bullheads comprise an insignificant 0.5 to 1.5 per cent of the annual catch in South Dakota waters, and Clark (1960) listed the black and brown bullheads as the least important species encountered in Lake St. Marys, Ohio, as reflected by annual harvest statistics. He added, however, that strong year classes occasionally appear, which assure well-balanced distribution of the species.

Important populations of bullheads and channel catfish *(I. punctatus)* formerly occurred in the Mississippi River and its tributaries. According to Barnickol and Starrett (1951), this species complex amounted to 50% of the commercial catch reported in 1899. This figure had dwindled to 15.1 per cent by 1946 corresponding to concommitant increases in the populations of other commercial species, particularly carp and buffalofishes (Barnickol and Starrett, loc. cit.).

Black bullheads have become prominent in small artificial lakes in many areas of the midwest (Jenkins, 1959), sometimes to such an extent that selective eradication projects have been directed toward population reduction (Houser and Grinstead, 1961). The greatest predominance appears to be in farm ponds where the management objective may or may not be bullhead propagation (Bennett, 1952). In Douglas County, Kansas, Hastings and Cross (1962) found black bullheads in 15 of the 22 farm ponds surveyed (68 per cent), and considered them as dominants in 14 of these.The ponds studied were aribtrarily classified on the basis of turbidity: 50 ppm or less suspended material constituted a clear pond, while one exceeding this limit was considered turbid. Black bullheads predominated in all turbid ponds for which quantitative estimates were obtained. Trautman (1957) found that black bullheads have increased in Ohio waters during the present century at the expense of other bullhead species. Increased siltation resulting from more intensively applied agricultural practices apparently has favored this replacement trend.

Differences in ponderal indices from different portions of Clear Lake, Iowa, suggested that several subpopulations could exist in the same body of water (Forney, 1955). Each of these subpopulations exhibited its own vital characteristics based, in part, on differences in food supplies. Various authors have attributed the distributional success of black bullheads to omnivorous feeding habits (Clay, 1962; Viosca; 1931; Smith, 1949), although Forney (1955) indicated that selective feeding occurred in Iowa. Rose and Moen (1951) concluded that selective feeding by adults was more apparent than real, usually reflecting the preponderance of one or more items over others in the food supply. Kutkuhn (1955) listed a variety of food items taken by adult black bullheads in Iowa lakes: insects, ento-

Foods taken by different age groups appear to differ significantly, resulting in part from differences in feeding times between adults and young. Darnell and Meierotto (1965) found that young-of-the-year bullheads school during the day, their social appetites stimulated by tactile and gustatory senses not shared by older individuals (Bowen, 1931). Adults were rarely active by day but commenced feeding with the onset of darkness and remained active throughout the night. Young bullheads (15 - 53 mm TL) in Clear Lake, Iowa, fed almost exclusively on Entomostraca (Forney, 1955). Ewers (1931) found that small bullheads (36 - 76 mm TL) in Buckeye Lake, Ohio, fed primarily on the amphipod *Hyalella*, Entomostraca and small insect larva, with peaks of feeding activity occurring just before dawn.

Feeding preferences appear to change sequentially with different stages of the reproductive cycle. Raney and Webster (1940), working with Cayuga Lake bullheads in New York, noted the following feeding pattern: adults moved into cover during periods of 50° to 55°F temperature (early April) and began feeding avidly on aquatic vegetation *(Nymphozanthus advena* and *Potamogeton)* prior to spawning. Throughout the remainder of the year, feeding habits were assessed as truly omnivorous. Forney (1955) noted a similar sequence, and concluded that plant feeding was somehow related to the attainment of reproductive readiness. He listed as staples throughout the first year of life, Crustacea (60 per cent) and Diptera larva (25 per cent, chiefly Chrionomidae). The inclusion of adult dipterans and bryozoan statoblasts suggested some surface feeding data, but such activity has not been described.

Age and growth statistics, vital to an understanding of any species' population complexities, have been reported from various states (Carlander, 1968); however, none have appeared representing the bullheads of Kentucky waters. Synthesis of the available material yields the following generalizations: growth tends to be more rapid in clear water, notwithstanding the black bullhead's propensity to dominate turbid waters (Hastings and Cross, 1962). Bullheads in Kansas and Iowa ponds tended to overcrowd turbid waters, rarely maintaining suitable growth rates. Houser and Collins (1962) noted slower growth rates in steeams than in ponds or reservoirs. Variations in growth rates have been so extreme throughout the range that comparisons for different habitat types are all but precluded (Carlander, 1968), as in the case of direct comparisons of Kentucky populations with others.

Albaugh (1969) found great intraspecific variability in growth per season. In artificial ponds provided with unlimited food supplies, males made greater gains than females, but when food supplies were kept near maintenance levels, growth rates were comparable. Simco and Cross (1966) reached similar conclusions concerning differential growth rates in *I. punctatus.*

Growth is apparently rapid during the first year of life, and subsequently slower coincident with the degree of intraspecific competition. Moen (1959) noted that bullheads in Silver Lake, Iowa, attained an average total length of 127 mm in September at age I, but only 132 mm (41 g) in September at age II. Following a severe winter kill, which significantly reduced competition, these same fish reached a length of 201 mm and 122 g at age III. The age IV group increased from 208 mm to only 213 mm at age V. Corthell (1961) assessed rapid growth of bullheads in the Empire Lakes, Oregon, as the result of recent introduction and low population density.

Some of the most worthwhile data pertinent to the management of scaled fish has been gained through the evaluation of age-growth relationships based on the scale method of age determination (Creaser, 1926; Buckman, 1929, Van Oosten, 1929). Since members of the genus *Ictalurus* lack scales, workers have resorted to annuli on bones and spines for age determination (Lewis, 1949, 1950; Forney, 1955; Carlander and Sprugel, 1948; Sneed, 1951). Houser and Collins (1962) found that annuli usually

formed on fin spines during the second week in May in Oklahoma waters. The uniform appearance of annuli from all age groups at the time indicated that all ages developed annuli at approximately the same time.

Few descriptions of the breeding behavior of *I. melas* are available. The early ichthyological notes of Fowler (1917) provided the following account. (It should be noted, however, that the author referred to the breeding pair simply as "bullheads", leaving some doubt as to their species identity.) "After a nest was constructed by the female, both sexes took charge of it; both guarded the eggs and the fry after spawning; and both were observed occupying the nest at the same and at alternate times. The deposited eggs numbered 200, were creamy white in color, and took approximately five days to hatch." Wallace (1957), in a more recent account, found that only the female excavated the nest. As the nest neared completion, each parent began to pay closer attention to the other. Actual spawning lasted for about one second, and occurred five times in a single hour. The female guarded the eggs during the first day, the male thereafter. Clemens and Sneed (1957) described a similar behavior in the channel catfish.

Black bullheads reportedly make no elaborate preparation for spawning, although gonadal development comprises a relatively long period of time. Dennison (1970) found reproductively mature males and females during the 1969 season in Clear Lake, Iowa, starting to mobilize material in the gonads for the next spawning season during August and September. Mesenteric fat was assumed to be the principal source of energy for gonadal development. Differences in the availability of mesenteric fat between the 1969 and 1970 seasons were reflected in the success of spawning and in fecundity indices.

Because of wide variation in weight at a given length within the rather narrow length range for mature bullheads, the value of the length-weight relationship as a measure of reproductivity is considerably reduced. Nevertheless, length has been used as an arbitrary index to reproductive readiness. Mississippi River bullheads with a total length of 154 mm or more, and belonging to age group III were considered reproductively mature by Barnikol and Starrett (1951). A similar range was proposed by Shields (1957a, b) for the bullheads of Gavins Point Reservoir, South Dakota. Dennison (1970) arbitrarily chose 229 mm total length as the size separating mature and immature bullheads in Clear Lake, Iowa.

Fecundity appears to be more closely related to length than to age. Clear Lake females, for example, 203 to 226 mm in total length contained and average of 3,283 eggs, while females of the same population 229 to 251 mm long contained an average of 3,845 eggs (Forney, 1955). Dennison (1970) noted a good relationship between length and fecundity in bullheads. Adult females with an average length of 250 to 259 mm had a mean fecundity of 3,892 eggs. Limits of fecundity throughout the range could not be determined, since few statistics, other than those listed above, are available (Carlander, 1968).

Few attempts have been made to establish the periods of reproduction for black bullheads. Chance observations of spawning periods have been the rule rather than the exception. Spawning occurs from late June to late July in South Dakota (Shields, 1957a, b). The earliest spent female was taken on June 26, and the latest ripe female on August 6, 1951 in Clear Lake (Forney, 1955). Dennison (1970) reported that the 1969 spawning season in Iowa extended from June 1 through July 1, while the 1970 season was somewhat shorter (June 10 to 23), each seasonal limit reflecting the influence of prolonged temperature increase.

The literature is incomplete with respect to environmental conditions that influence initiation of the spawning response. Buser and Blanc (1949) tested the effect of photoperiod on gonadal development in *I. nebulosus*. Continuous light in winter produced increase in testicular and ovarian weight, accompanied by increased in the deposition of interstitial tissue. According to Burger (1939) and Medlen (1951) temperature was a more influential factor than light for a number of fishes (see also, Liley, 1969; Har,

1965). Wallace (1967) observed spawning in captive bullheads that had been retained in the laboratory from August through March. Environmental conditioning was not intended, i.e., photoperiod control was not maintained, and temperature was held at a constant 25°C. The absence of control did not inhibit induced spawning. Dennison (1970) stated that spawning was triggered by an abrupt increase in water temperature, ranging from 6° to 8°C over a period of several days.

Any fish that lives in farm ponds is subjected to seasonal and sudden changes in temperature, but not necessarily in light intensity (Wallen, 1955). The Secchi disk visibility in Oklahoma ponds, determined on 132 occasions from 1951 to 1954 averaged only 45.7 cm. Readings of 6 mm, varying slightly throughout the year, were recorded for some turbid waters known to contain bullheads.

Accounts of black bullhead embryonic development are scarce. Spawning seems difficult to induce in the laboratory, since even reproductively mature individuals often become refractory under imposed conditions (Sneed and Clemens, 1960). To avoid this difficulty, especially where regulation of spawning is economically important, several methods have been devised to heighten or induce spawning. The dependence of sexual behavior on the gonadal secretions of fish is well-authenticated (Jones and King, 1952; Cohen, 1946; M.C. Tavolga, 1949). There is, however, experimental evidence to indicate that sexual behavior and spawning attempts may be influenced by pituitary hormones in the absence of gonadal mediation (Noble and Kumpf, 1936). Hypophysectomy, on the other hand, can cause the complete cessation of the behavioral sequence which normally leads to spawning (W.N. Tavolga, 1955).

An authoritative review of the role of pituitary hormones in spawning, and the use of excised pituitary glands in pisciculture has been presented by Pickford and Atz (1957), and specific accounts have appeared periodically (Robinson and Rinfret, 1957; Schmidt, et al. 1965; Graybill and Horton, 1969). Sneed and Clemens (1957) dealt with induced catfish spawning, a method used successfully to influence the sequence of bullhead reproduction by Wallace (1967).

Several investigators have commented on the ability of black bullheads to survive in waters that are uninhabitable for most other species (Black, 1953, 1955; Lewis, 1949; Trautman, 1957; Bennett, 1948). Bullheads have apparently evolved certain adaptive mechanisms which elevate tolerance levels in contrast to less hardy species. Hathaway (1927) found little change in feeding and behavior patterns with markedly increased water temperatures, and Bailey (1955) described the chance observation of mass-mortality in Bass Lake, Michigan. Death to a complex of species was assessed as the result of high temperature, since none of the characteristic signs of anoxia were apparent. Ictalurid fishes were the least affected; a water temperature of 38°C was not limiting to the catfishes so long as free movement was assured.

Temperature relation analyses of poikilothermic animals are extensive in the literature (Bullock, 1955; Precht, et al. 1955). Brett (1956) measured the median resistance times of several species of fish that were tested at various high temperatures and acclimated at 20°C. The upper incipient lethal temperature (the point at which no further death occurred with time) for *I. nebulosus* fell between 32°C and 33°C. Morris (1965) reported similar information for the yellow bullhead, a species he found adaptable to extremes of both heat and cold. Black (1953) found that black bullheads acclimated at 23°C had an upper lethal temperature of 35°C, but she failed to report the effects of cold and associated lethal temperatures.

Cowles and Bogert (1944) introduced the concept of critical thermal maximum (CTMax). According to these authors, upper lethal temperatures have little ecological significance, since species in nature will usually be prevented from reaching extremes. The critical thermal maximum was subsequently defined as the thermal point at which locomotory activity becomes dis-

organized, and the animal loses the ability to escape conditions that would promptly lead to its death. According to this definition, physiological and ecological death points do not necessarily coincide, and may, in fact, be widely separated. A similar argument could be posed for critical thermal minimum (CTMin).

The ecological significance of temperature thresholds in fish has been questioned by Hart (1952) and Brett (1959), who contended that temperature tolerances are usually well above habitat extremes. Critical thermal determinations that reflect the ecological rather than physiological death range have also been considered more valid than incipient lethal temperatures by Lowe and Heath (1969). Few CTM determinations have been made for freshwater fish, presumably because of the difficulty associated with determination of the ecological death point (Hutchison, 1961; Norris, 1963).

Forbes and Richardson (1909) stated that bullheads cease feeding and become sluggish, sometimes burrowing into the mud, in late fall. Underhill (1952) demonstrated that, although brown bullheads acclimated to 10°C showed reduced rates of feeding, they did continue to feed throughout the year, and Nordlie (1966) noted that black bullheads, which remained relatively active throughout the winter, had peptic digestive rates that could be correlated to acclimation histories. The extent to which other physiological functions depend on temperature, and the limits to which these dependences can be expected to adjust, have been poorly authenticated for ictalurid fishes.

Prosser and Brown (1962) reported that fish approximately double their oxygen requirements for every 10°C rise in temperature. Thus, it is important from the standpoint of total metabolic expenditure for fishes to enjoy acclimation in gradients of both temperature and dissolved oxygen. According to Brett (1944), however, acclimation from 3.9° to 13°C took approximately 20 days in the goldfish *(Carassius auratus* Linnaeus), and may have been even slower for the reciprocal gradient. To compensate the need for continuous acclimation, fishes seek optimum temperatures (at which metabolic oxygen demand is probably also optimum) and tend to congregate there (Dendy, 1945, 1946; Buck and Cross, 1952; Brett, 1944; Fry and Hart, 1948a, b). Preferred temperatures have been determined for a relatively few fish species (Fry and Hart, 1948a), and not at all for the black bullhead. Morris (1965), opposed to Brett's (1944) observation, noted that *I. natalis* adjusted rapidly to different acclimation temperatures by invoking compensatory metabolic adjustments. When moved to water at 27°C, a fish acclimated at 12°C, lowered its metabolic level from 0.35 to 0.15 ml O_2/hr.

Active metabolism of some fish *(Salvelinus* sp.) may be four times the resting rate (Fry and Hart, 1948a). The activity patterns and distributional success of fish were most often reflected by their metabolic rate. For example, percid darters have several times greater metabolic rates than most sluggish fish (Vernberg, 1954).

Caillouet (1967a) concluded that death of channel catfish following hyperactivity was caused, at least in part, by lactic acidosis. However, Black (1955) and Caillouet (1967b) suggested that increased blood lactic acid in exercised black bullheads was insufficient to cause this condition. Black (1955) attributed this to a low Bohr Effect, i.e., increase in blood lactic acid had little effect on the oxygen combining capacity of the blood. Buddenbrock (1938) suggested lactic acid concentration might lead to tissue hypoxia. Thus fish with relatively low metabolic requirements, enjoying the advantage of a low positive Bohr Effect, should be favored in situations where the dissolved oxygen-carbon dioxide ratio imposes hypoxial limits on less favored species.

Early studies by Birge (1907) showed that waters in which dissolved oxygen was abundant produced no gas other than carbon dioxide in appreciable amounts. McCay (1925) and Powers (1937) implicated carbon dioxide in fish poisonings. This gas is important from the standpoint of its relation to gas exchange at the gills – since it cannot be excreted osmotically against a gradient – and in its relationship to the oxygen combin-

ing capacity of the blood and the premature unloading of oxyhemoglobin (Matthew, 1921). W.G. Moore (1942) measured the oxygen regimens of 13 species of fish by suspending them in live boxes at various depths. Black bullheads were the least susceptible to hypoxia at the highest carbon dioxide tensions encountered. Even the brown bullhead was unable to endure oxygen tensions of 2.8 to 3.7 ppm for 24 hours in waters of high carbon dioxide tension. Powers, et al. (1938) showed that fishes could absorb oxygen to low levels in wide ranges of carbon dioxide. The species *Micropterus dolomieui* Lacépède, *Ambloplites rupestris* (Rafinesque) and *Perca flavescens* (Mitchill) were able to extract oxygen down to 0.30 and 0.40 ml/l in carbon dioxide tensions of 0.15 to 21.00 mm Hg. Comparable data for ictalurid fishes have not been presented.

Natural mortality for a given body of water, and species complex, during a specific period of time, appears to be one of the most difficult of all fish population parameters to estimate with any degree of statistical accuracy (Ricker, 1944, 1958; Regier, 1962). Two basic analysis procedures have been proposed and subsequently elaborated to provide mortality estimates. The first provides estimates for populations that obey certain well-defined restrictions: the population must remain unexploited throughout the study period; it must be affected by neither recruitment nor emigration; it must be assumed homogeneous with respect to species and age. The second method is designed to provide estimates for exploited populations and becomes rather involved by comparison. It is not surprising, then, that few attempts have been made to estimate differential mortality in freshwater situations. It is usually difficult to observe a population in extensive enough detail to assure than the necessary assumptions have been met. As a result, most of the mortality that has been reported has been of the chance observation type; however, even this type of information can prove important to the management of a fishery (Bailey, 1955).

Bennett (1948) sampled Gale Lake, Illinois, previous to and after a known winter-kill during which approximately 80 per cent of the population was decimated. Analysis of the persistent population pointed to a conclusion now basic to fisheries management; population mortalities are seldom, if ever, complete, and the remaining portion can radically alter the fishery condition. Gale Lake bullheads, along with carp and buffalofish, survived the mass-mortality, and subsequently proliferated to such an extent that the lake no longer provided sport fishing. Powers (1937) commented on the factors involved in the sudden mortality of fishes, relating the aperiodic influence of bacterial oxygen depletion-carbon dioxide elevation curve to unexplained fish kills, and conjectured "derangement" resulting from continuous adjustment to different carbon dioxide tensions as an important mortality factor.

MATERIALS AND METHODS

Study Area Characteristics

Sample populations utilized during this study were contained within the adjoining central Kentucky counties of Madison, Fayette and Clark in the Kentucky River drainage. The area is underlain by Ordovician and Silurian limestone (Hall and Palmquist, 1960). Elevation ranges from 500 feet on valley floors to as much as 1,000 feet on ridge-tops on shale and limestone hills; major drainages range in elevation from 800 to 900 feet. Graybrown podzolic soils underlain by soft limestone or highly calcareous shale are conspicuous on steeper ridges (Austin, 1965).

The continuity of underlying strata lends some degree of similarity to major streams and artificial impoundments throughout the area, but differences in topography and land-use patterns affect stream habitats and the faunal complexes they contain. Consequently, several streams were surveyed before the study areas listed below could be chosen. Since it was desirable to compare certain data from different habitat types, the bullhead populations of Wilgreen Lake and several smaller impoundments were also utilized.

Streams:

Streams throughout the study area were surveyed to ascertain the character of their bullhead populations. Two of these, Boone Creek in Clark and Fayette counties, and Strodes Creek in Clark and Bourbon counties, were considered to have suitable bullhead populations. The Boone Creek drainage consists of first through fifth order streams from its headwater just north of U.S. Route 60 to its confluence with the Kentucky River, 0.8 km east of Clay's Ferry, Kentucky. Land adjoining lower order streams (first through third) was being utilized primarily as permanent pasture, with only a small portion under crop tillage. Third order streams contained numerous silt bottom pools that proved excellent habitats for isolated populations of black bullheads. Two third order tributaries, the East and West forks of Jones Creek, which converge approximately 10 km from the intersection of Cleveland and Sulfur Well roads, were sampled through the study period.

Strodes Creek, located north of Winchester, Kentucky (38° 02' latitude; 84° 12' longitude), is a tributary of Stones Creek which, in turn, flows into the South Fork of the Licking River in Bourbon County. The entire southern drainage joins the main fork of the Licking River at Falmouth, Kentucky. The streams in this drainage, especially Strodes Creek and its tributaries, are maximally influenced by agricultural use. Meandering stream beds are extensively silted, pools are abundant and stream flow is minimal during most of the year. All tributaries sampled contained large numbers of black bullheads. Johnson Creek, the most prominent tributary of Strodes Creek, was sampled during the spring and summer of 1971.

Ponds:

Farm ponds, and other small earthen impoundments, were surveyed to determine the feasibility of their use for this study. Seventeen ponds were considered; of these, the five listed below were found to contain black bullhead populations and were selected for further study. Ponds I, II, and III were located on the Central Kentucky Wildlife Management Area situated 4.2 km east of Kingston, Kentucky (37° 38' latitude; 84° 14' longitude). Pond IV was located on Fairview Farm approximately 2.4 km south of the intersection of state routes 1156 and 25 near Whitehall, Kentucky. Pond V was in Fayette County, Kentucky, 0.8 km south of state route 421 at 37° 54' latitude; 84° 20' longitude.

Pond I: This pond had a surface area of approximately 0.65 acre (.26 ha), with a maximum spring depth of 2 m. The entire surface area was of open water; no marginal or emergent vegetation occurred. The pond accepted run-off from a denuded 3.0 acre barnlot.

Pond II: Formed within a natural valley approximately 0.4 km wide, this pond had a surface area of 0.5 acre (.20 ha) and a maximum depth of 2.6 m. It received a spring-fed stream which flowed throughout the study period. Emergent vegetation (primarily *Sagittaria* sp. and *Scirpus* sp.) and mats of filamentous algae (*Spirogyra* sp.) covered approximately 25 to 30 per cent of the surface through spring and summer. The bottom deposits consisted of pulpy peat and muck that reached depths of 0.9 m.

Pond III: This pond was small and shallow, with a surface area estimated at 0.125 acre and maximum spring depth of 1.0 to 1.2 m. It was located within a natural depression that contained some water throughout the year, but received the flow from adjoining pastures only during heavy rains. Emergent vegetation (predominantly *Sagittaria* sp.) was prominent over the entire surface.

Pond IV: With a surface area of 0.50 (.20 ha) acre and a maximum depth of 1.5 m, this pond also drained pastured areas. Aquatic vegetation was limited to insignificant accumulations of pondweed (*Potamogeton* sp.); however, during spring and early summer it was extensively covered with algal mats (*Spirogyra, Oedogonium* and *Zygnema*). Bottom deposits were of ooze to a depth of 1.0 m.

Pond V: This was a pond of recent origin (four years) located at the base of a natural valley. The open water area covered approxi-

mately 0.25 acre (.10 ha) acre, and the maximum spring depth was 1.5 m.

Lakes:

Wilgreen Lake, formerly known as Taylor Fork Lake, is located in Madison County, Kentucky, with spillway and access point located approximately 4 km from the intersection of Barnes Mill and Curtis roads (37° 54' latitude; 84° 20' longitude). The lake has been inadequately surveyed surveyed; consequently most morphometric data has not been detailed. The shore line extends an estimated 42 km, containing 175 surface acres of water (71 ha). The early spring maximum depth was between 24 and 26 m. Shoal areas (water less than 1.2 m deep) comprised an estimated 15.0 to 20.0 per cent of the total area: aquatic vegetation, other than filamentous algae, was conspicuously lacking from shoal waters. Wilgreen Lake was sampled during the period July 1970 to June 1971.

Capture Methods

Several methods were employed to capture specimens. Most pond sampling was during winter months (Nov. 1970 to Feb. 1971) using wire traps. Larvae and young-of-the-year were sampled by means of a modified meter net, and by hand netting along shore-lines. Stream populations were sampled with a 15 foot (4.57 m) common-sense seine of 1/4 inch (6 mm) linear mesh. Samples were taken from Wilgreen Lake during the fall of 1970, and from February through June 1971, using: 5-cm inner mesh trammel nets established across major channels; wing nets, 3.8- and 2.5-cm mesh funnels and 1.3-cm wings, fished in waters less than 3 m deep: bag seines trawled in affluents and shallow coves: and 230-volt electric shockers operated along shore.

Population Dynamics

Food Habits. Food habits were assessed for all populations studied, i.e., from ponds, lakes and streams, and for all age groups within the populations. The terminology of Hubbs (1943) for establishing age classes was followed. According to this analysis, transition from lower to higher age class occurs on either January 1 or July 1 (Hile, 1948). Since the black bullheads in this study were found to form annuli during the month of June, July 1 was used as the transformation date.

To determine feeding selectivity, benthic and planktonic analyses were carried out during all seasons of the year, and the results scaled to reflect annual availability. The weighted percentage of availability was then compared to percentage estimates of appearance of the same items in the stomach contents of representative samples to form an electivity ratio for each item. The electivity ratio used by Priegel (1970) is represented by the equation:

$$E = \frac{r_i - P_i}{r_i + P_i}$$

Where r_i is the relative percentage of any food item in the stomach, and P_i is the relative percentage of the same item available to the fish.

Values of (E) range from –1 to +1, and a value of 0 was expected for a food item when no selective process was operative. Invertebrate identification followed Eddy and Hodson (1961) and Pennak (1953).

Age and Growth. Representative samples from all study areas were investigated to determine age and growth characteristics. Age determinations were made by modifications of procedures suggested by Lewis (1949) and Sneed (1951). Lewis aged black bullheads by viewing the annular markings on vertebral centra, and Sneed was able to age channel catfish by the number of annular depositions on pectoral and dorsal spines. In the latter case, these sections were made near the base of spines, a drop of xylol added, and the preparation viewed under indirect light. In this study a more facile modification of Sneed's procedure was successfully employed. Instead of making a thin section, the pectoral spine was simply severed near its base with a high-speed rotary cutter (Dremel Model 42), the cut portion polished if necessary by the use of a high-speed jeweler's stone, and the entire spine mounted in styrofoam for observation under

indirect light. Age estimates, when compared to preparations by Sneed's method (1951), were identical.

Total length (tip of snout to tip of tail) and a standard length (tip of snout to the flection point at the caudal peduncle) were determined on a standard mm-measuring board. All weights were determined on a tri-beam balance permitting a precision of ±0.05 g.

The coefficient of condition (K) was determined for representatives of pond, lake and stream populations. The condition factor was that proposed by Hile (1936), represented by the equation:

$$K = \frac{100W}{L^3}$$

where, K is the coefficient of condition, W is the weight expressed in grams and L is the standard length expressed in centimeters.

Since the coefficient of condition was designed as a comparative value, it has little significance as an absolute number.

Weight-length relationships for each habitat were determined according to the expression Log W = a + n Log L, where W is the weight in grams and L is the length in millimeters. The resultant regression equations were analyzed as to the homogeneity of their slopes. In addition, correlation coefficients were employed to establish the relationships between weight and length, age and weight, and age and length for each population.

Population Estimates. Population estimates were made for pond populations to relate degree of crowding and intraspecific competition to population success. These estimates were made by employing the mark-recovery procedure detailed by Fredin (1950) which modifies the Peterson method by considering each sample as a separate estimate. By this method, usually referred to as a Schnabel estimate (Ricker, 1975), a more accurate estimate is assured by the process of minimized squares according to the expression (where marking is continued into the recapture period):

$$N = \frac{S\, n^2 (m + u)}{S\, (nm)} \qquad (1)$$

where, N is the total population estimate, m is the number of fish marked during the first sampling period, u is the number of unmarked fish in the second sample, n is the number of marked fish in the pond, and S represents summation.

Ricker (1958) noted that (1) was most efficient when the value n/N was 0.5. Where this assumption could not be made, and in cases where subsequent estimates were made over long periods of time (one month or more), the standard Petersén mark-recovery index was utilized (valid only if M is constant). According to this procedure, the total population (P) is equal to a ratio of the number of marked and unmarked fish in a pond according to the expression:

$$P = M (U + R)/R$$

where, M is the number of fish marked during the first sampling period, U is the number of unmarked recoveries and R is the number of marked recoveries.

Natural Mortality. The bullhead population in Pond I was followed throughout the study period to set limits on the extent of natural mortality, and to determine the period or periods when fish are most vulnerable to the factors of natural mortality. The procedure used to calculate natural mortality followed those of Regier (1962) for exploited populations, and will not be detailed here. Although this pond was not exploited through fishing effort, sampling in the pond was considered exploitation, and the mortality was analyzed accordingly.

Reproductive Potential

Gonadal Development. Fish were removed from Pond I and II during the period August 1970 through July 1971 to obtain an index for male and female gonad development after procedures suggested by Larimore (1957). Since Dennison (1970) established gonad development curves for male and female black bullheads in a lake population, greater emphasis was placed on pond

development during this study. However, estimates were made throughout the spring and summer of 1971 for lake and stream populations, and the results were superimposed on pond fish curves. The gonadal development index is simply a ratio of gonad weight to body weight. Samples from ponds were analyzed at bi-weekly intervals from August 1970 through February 1971, and weekly thereafter. From these values the high and low points of the reproductive cycle were determined. In addition, gross morphology of the gonads was described for each stage in the development sequence.

Fecundity. The several methods used for analysis of egg production in fish (Davis and Paulik, 1965; Boyar and Clifford, 1967; Behmer, 1969; Larimore, 1957) can be grouped under three headings: dry weight measure, volumetric measure, and egg displacement. Each of these methods was analyzed in contrast to total egg counts to determine the most suitable method for bullhead fecundity determinations (Table I). Subsequently, all determinations were made by the egg-weight and displacement methods of Burrows (1951b); the dry-weight method was excluded. Since all methods tested overestimated the actual number of eggs (minus any adhering germinal tissue), all determinations were corrected by factors corresponding to the magnitude of over-estimation. Displacement determinations were multiplied by a factor of 0.90, volumetric methods by 0.79, and egg-count determinations by a factor of 0.98 (Table I) to account for adhering germinal tissues. All weights obtained during this procedure were determined by means of a Mettler 400 analytical balance with ±0.0005 g precision.

Induced Spawning. Eight pairs of black bullheads, designated as possible spawners, were brought into the laboratory and segregated into breeding pairs. The fish ranged in weight from 130 to 145 g, and in standard length from 168 to 220 mm. They were maintained on a diet of adult crayfish reinforced with liver. The male and female of each pair were separated from each other in 50-gallon (189 l) aquaria by imposing 1.25 cm mesh weld-wire partitions. The photoperiod was varied according to the environmental photoperiod, and temperature was increased at the rate of 1°C per day to a maximum of 27°C.

In accordance with a procedure detailed by Sneed and Clemens (1960), each pair was treated with dried carp pituitary which had been previously prepared by desiccation in four 12 hour changes of acetone, then stored in sealed vials. Each fish received 4.0 mg dried pituitary per 24 hour period until signs of pre-spawning behavior appeared, or for a total of 10 intramuscular injections. Pituitary glands used in the study were obtained from carp seined or trapped in local streams; these were not separated as to sex or stage of reproductive development. Pituitaries used were not over two hours old when dried.

Physiological Ecology

Oxygen Consumption. Oxygen consumption rates were determined for age groups post-larva through age group I (to formation of second annulus) at three acclimation temperatures, 7°, 12° and 23°C. Acclimation was accomplished for each group by subjecting ten or more fish to progressively decreasing temperatures in a Sherer-Gillett Environmental Chamber. Once the desired temperature was reached, fish were held at this temperature for an additional 7 to 10 days. Notably, however, post-larval specimens (approximately 2 days post-hatching) could not be acclimated to 7°C. Consequently, determinations for this group were made only at 12° and 23°C.

Oxygen consumption rates (standard rates) were determined by immersing fish held in weld-wire cages consistent with their total length, into 5.54 liter glass aquaria. The aquaria were sealed with a plexiglass cover and silicon sealant, and filled to capacity through a single 7.5 mm hole drilled to accept the BOD probe from a YSI Model 54 Oxygen Analyzer. Subsequent to filling, fish were allowed to accustom themselves until locomotory activities minimized before initial oxygen readings were made. Prior to each experimental run, demineralized water in the chambers was recharged with oxygen to a level of 8.0 to 9.0 ppm. (Oxygen con-

Table 1. Preliminary analysis of egg count methods. Column A= total counts; Column B= estimation by displacement methods; Column C=estimation by volumetric methods; Column D= individual egg weight method. SL= standard length (mm); D= deviation from total count; $\overline{X}$= mean of deviations.

SL	LOCATION	A TOTAL COUNT	B ESTIMATE	B D	C ESTIMATE	C D	D ESTIMATE	D D
169	POND	1891	1923.0	+32	2312.5	+493.5	1900	+9
176	POND	1927	1985.0	+59	2404.0	+477.0	1943	+16
176	POND	1914	1922.0	+8	2322.0	+408.0	1923	+9
210	POND	2880	3845.0	+965	3520.0	+640.0	2992	+112
156	POND	1600	1748.0	+148	2104.0	+405.0	1623	+23
195	POND	2880	3312.0	+432	3415.0	+535.0	2903	+23
177	POND	3015	3150.0	+135	3271.0	+156.0	2975	+40
		$\overline{x}$ = 2301.0	$\overline{x}$ = 235		$\overline{x}$ = 473.4		$\overline{x}$ = 33	
			% dev = 10.21		% dev = 20.54		% dev = 1.75	
		Correction Factor =	100 - .1021 (.90)		100 - .2057 (.79)		100 - .0175 (.98)	

sumption rates were read in mg O_2/g/hr for purposes of comparison.) Consumption rates at the three acclimation temperatures were expressed as functions of stage of development, and the corresponding Q_{10} values between each pair of acclimations were established according to the equation of Prosser and Brown (1962). In addition, oxygen consumption per fish was expressed as a function of weight at 23° and 12°C. For age groups with weight ranges greater than two standard errors of mean weight, consumption rates were converted to the rate of an individual of mean weight according to the equation:

$$M_m = (W_m^a \times M)/W^a$$

Where, M_m is the metabolic rate of a mean weight fish, W_m is the mean weight, M is the metabolic rate of any fish in the sample, W is the weight of any fish in the sample, and a is the slope of the weight versus consumption rate curve for any size group (Smit, et al., 1971).

In addition to routine rates, oxygen consumption was measured as a function of decreasing oxygen tension and increasing carbon dioxide tension in order to establish threshold values. Water used for these procedures was first "stripped" of oxygen down to 4.0 ppm (2.8 ml/l at 20°C) by subjecting it to a jet of nitrogen gas. Fish were then allowed to spontaneously reduce oxygen levels to near-asphyxiation levels. Rates were continuously monitored by a procedure analogus to that described above.

Temperature. Lower incipient lethal temperatures, critical thermal maxima and temperature preference ranges were determined at the three acclimation temperatures listed above. Lower lethal temperatures were established by subjecting groups of ten or more fish (post-larva through age II) to progressively high temperatures from a minimum corresponding to the freezing point of water. The point in time at which 50 per cent mortality (LT_{50}) occurred was recorded, and the temperature at which no further death occurred with time was considered the lower lethal temperature. While under observations the fish were disturbed only for periodic aeration of the water.

Critical thermal maxima (incorporated into the data analysis as upper lethal temperatures) were determined by a procedure similar to that described by Hutchinson (1961). Tri-necked distillation flasks were fitted into hemispherical heating mantles which could be heated at any desired rate by means of a variable voltage transformer. Animals to be tested were placed in sufficient demineralized water to allow free movement. Alternate ports of the flask were provided with an air hose to aerate and circulate the water, and the probe from a YSI Model $4S_2$ Tele-Thermometer. Temperatures were recorded at the beginning of each run (t_o) and at the CTMax (tf), which was the point at which an animal failed to maintain an upright position. All animals used for CTMax determinations were acclimated at 7°, 12°, and 23°C for periods of 7 to 10 days. Subsequent to determination, the previously unfed animals were allowed to recover in water held at their prior acclimation temperature.

Temperature preference ranges were determined for age groups post-larva through age I, since design of the apparatus did not facilitate the handling of older fish. Animals previously acclimated to the temperatures designated above were placed in a 10-foot galvanized gradient chamber. The chamber, located in a walk-in refrigerator of 5° ambient temperature, was so constructed that temperature could be graduated from 3° to 27°C through 12 previously marked intervals. Ten to fifteen animals of comparable age and size were placed in the chanber at the point corresponding to their prior acclimation temperature. At hourly intervals, for a total of nine hours, the animals were observed and their positions in the gradient recorded. This was easily accomplished without causing disturbance, since the fish could be observed from outside the refrigerator. In order to eliminate light as a factor in range selection, determinations were made under full illuminations on fish previously acclimated to constant light.

Correlative Studies. In conjunction with laboratory and field studies, water chemistry analysis was accomplished for each habitat sampled following Hach Chemical Company procedures. Table 2 contains a complete listing of determinations, and the range of each year specified periods of time.

Statistical analyses followed the procedures of Sokal and Rohlf (1969), and Downie and Heath (1961).

RESULTS

During the period July 1970 through July 1971, a total of 623 adult black bullheads (age groups I through VI) was taken from the study area. Fifty-six per cent of these (349 specimens) were obtained from ponds, 36% (224 fish) from streams, and the remaining 8% (50 fish) from Wilgreen Lake. In addition to adults, 300 post-larvae and juveniles were taken from the three habitat types.

Food items consumed by 292 adult black bullheads, the availability of each item in the habitat expressed as a weighted volume per cent, and the corresponding electivity ratio of each, are presented in Table 3. Although a great variety of food items was taken by adults, there was evidence to suggest feeding selectivity. Table 3 shows that chironomid larval and pupal stages made up a predominant part of the adult diet; however, this item had no greater selection value (0.1 to 0.5) than some other less common foods.

Food items taken most frequently differed from one habitat to another. Pond populations took chironomids and additionally relied heavily on physid and

Table 2. Water chemistry analysis of ponds I, II and IV, Wilgreen Lake and Boone Creek for the months indicated within the period, June 1970 through July 1971. All concentrations are in averages and ranges expressed as parts per million (PPM). Temperature is expressed in° C.

	Period of Observation	D.O.	CO_2	Methyl Orange Alk.	T Hardness (ppm $CaCO_3$	pH	Turbidity	H_2S	NH_3 Nitrogen	Temp. °C
BOONE	April, 71	9.8-13.4	0-2.0	132-200	152-206	8.0-8.9	0.5-7.5	*	*	16-21.5
CREEK	May, 71	9.8-12.6	0-7.0	116-172	160-238	6.4-6.9	0.5-6.8	*	*	17.5-23.0
	June, 71	6.8-11.2	0-2.0	130-164	182-195	6.5-7.5	3.0-10.2	*	*	19.0-26.0
WILGREEN	March, 71	11.5-13.0	5.0	*	*	6.0	*	*	*	5.5-8.9
LAKE	April, 71	10.0-13.0	5.0	*	*	6.5	*	*	*	9.0-15.6
	May, 71	2.3-10.2	5.0	82-134	120-165	7.0	4.0-7.2	0.1-1.5	0.7-0.9	15.0-25.5
	June, 71	0.4-11.7	5.0	62-146	106-175	6.5-6.9	4.0-20.0	0.2-0.5	0.6-1.0	18.0-30.0
POND I	June, 70	4.9-7.7	5.0	84-88	84-88	6.5-6.8	140	0.2	1.04	18.5-25.0
	July, 70	3.9-6.0	7.4	84-94	96-116	6.2-6.9	100	0.3	1.66	25.0-29.0
	August, 70	3.0-6.8	9.4	84-102	90-116	6.0-6.9	100	0.4	1.78	25.0-29.0
	September, 70	3.9-6.0	8.4	88-102	48-90	5.4-6.3	84	0.2	1.60	23.2-29.0
	October, 70	8.0-12.0	7.3	66	56-92	5.4-6.0	84	0.2	1.08	14.5-20.2
	November, 70	10.0-13.5	5.0	82	58-88	6.0	84	0.1	0.70	9.5-14.8
	December, 70	10.5-14.0	5.0	*	*	7.0	*	* *	*	6.0
	January, 71	14.0	5.0	*	*	7.0	*	*	*	5.0
	February, 71	14.0	5.0	*	*	7.0	*	*	*	4.0-5.0
	March, 71	13.5-14.0	5.0	70	76	6.5-7.0	76	0.0	0.00	5.0-9.0

	Period of Observation			Methyl Orange Alk.	T Hardness (ppm $CaCO_3$	pH	Turbidity	H_2S	NH_3 Nitrogen	Temp. °C
	April, 71	9.3-10.4	5.0	84	140	6.0-6.2	80	0.1	0.30	9.0-13.0
	May, 71	8.5	15.0	84	148	6.2	85	0.0	1.78	13.0-17.0
	June, 71	4.7	7.5	84	140	5.8-6.5	80	0.2	1.78	17.0-28.0
POND II	June, 70	8.9-10.0	5.0	88	112	6.5	12	0.0	0.20	16.2-19.0
	July, 70	7.5-9.0	5.0	84	100	6.5	19	0.0	0.20	17.8-21.0
	August, 70	6.0-8.5	5.0	84	96	6.0	23	0.0	0.30	19.4-23.5
	September, 70	6.5-8.5	5.0	88	100	6.5	25	0.0	0.10	17.5-26.0
	October, 70	12.5	5.0	84	92	6.0	12	0.0	0.00	16.8-23.5
	November, 70	13.5	5.0	84	92	6.0	15	0.0	0.00	12.9-17.0
	December, 70	14.2	5.0	*	*	6.2	*	*	*	7.4-12.0
	January, 71	14.0	5.0	*	*	6.0	*	*	*	6.5
	February, 71	13.8	5.0	*	*	6.5	*	*	*	5.5
	March, 71	12.5-14.0	5.0	102	122	6.2-6.9	31	0.0	0.00	6.0-10.0
	April, 71	10.9-13.0	6.0	88	100	6.0-7.0	19	0.0	0.00	10.0-15.0
	May, 71	9.5-12.5	5.0	84	96	6.0-7.0	19	0.0	0.10	10.0-15.0
	June, 71	8.5-11.9	7.4	90	100	6.5-7.2	19	0.0	0.10	19.0-26.0
POND IV	April, 71	6.3-7.5	8.5	*	*	7.0	104	0.5	0.75	*
	May, 71	4.9-5.5	11.7	*	*	5.8	112	0.5	1.35	*
	June, 71	2.5-4.9	14.0	*	*	6.0	140	0.5	1.78	*

* not determined

Table 3. Food consumption of 292 adult black bullheads expressed as (A) percentage of total complement, (B) represents percentage of each item available and (C) is the electivity value of each available item.

Food Organism	Ponds			Wilgreen Lake			Streams		
	A	B	C	A	B	C	A	B	C
Annelida									
Oligochaeta	6.1	1.5	0.6	8.8	3.5	0.4	2.9	1.9	0.2
Pelecypoda									
Spaeriidae	3.2	12.4	-0.6	0.4	7.4	-0.9	13.1	15.3	-0.1
Gastropoda									
Planorbidae	2.1	0.8	0.5	2.8	5.5	-0.3	2.9	1.4	0.4
Physidae	5.5	0.8	0.7	16.0	5.5	-0.6	5.8	6.4	-0.1
Rotifera	0.0	3.2	-1.0	0.0	7.8	-1.0	0.0	*	...
Cladocera	0.0	9.3	-1.0	0.0	12.5	-1.0	0.0	*	...
Copepoda	0.0	6.5	-1.0	0.0	3.5	-1.0	0.0	*	...
Ostracoda	0.0	1.3	-1.0	0.0	7.8	-1.0	0.0	*	...
Amphipoda	1.4	2.5	-0.3	4.9	1.7	0.4	2.9	5.3	-0.3
Isopoda	0.0	1.1	-1.0	0.0	0.3	-1.0	0.7	0.5	0.2
Decapoda	1.5	1.5	0.0	0.0	0.6	-1.0	5.1	7.8	-0.2
Ephemeroptera	1.5	0.3	0.6	1.1	1.1	0.0	3.6	2.9	0.1
Plecoptera	0.0	0.0	...	0.0	0.0	...	1.5	1.1	0.2
Odonata									
Zygoptera	3.0	2.1	0.2	4.2	1.1	0.6	0.7	2.0	-0.5
Anisoptera	6.7	1.5	0.6	2.1	1.9	0.1	3.6	3.0	0.1
Trichoptera	0.0	0.0	...	0.0	0.0	...	3.6	2.9	0.1
Diptera									
Chironomidae	47.2	45.2	0.0	55.5	19.3	0.5	39.0	11.9	0.5
Tabanidae	2.3	0.6	0.6	0.0	0.5	-1.0	0.7	0.1	0.7
Tipulidae	0.0	0.0	...	0.0	0.0	...	3.6	0.7	0.7
Simulidae	0.0	0.0	...	0.0	0.0	...	8.0	2.9	0.5
Unidentified	2.0	0.8	0.5	4.9	1.4	0.6	0.0	0.0	...
Hemiptera									
Corixidae	0.0	0.8	-1.0	0.0	0.9	-1.0	2.2	1.4	0.2
Amphibia									
Ranidae (Larva)	1.5	1.8	-1.0	0.0	0.0	...	0.0	*	...
Pisces									
Lepomis macrochirus	3.8	5.6	-0.2	0.0	*	...	3.6	3.6	0.0
Micropterus salmoides	2.3	0.5	0.7	0.0	*	...	0.0	*	0.0
Pimephales promelas	13.0	7.8	0.3	0.0	*	...	2.2	1.0	0.4
P. notatus	0.0	0.0	...	0.0	*	...	2.9	4.6	-0.3
Cyprinus carpio	0.0	0.0	...	0.0	0.0	...	0.7	0.2	0.7
Notropis sp.	0.0	0.0	...	0.7	*	...	8.0	7.4	-0.4

* Density Not Determined

planorbid snails, sphaeriid clams, dragonflies and the young of fish species (especially the minnow *Pimephales promelas*). Adults from Wilgreen Lake consumed appreciable numbers of the amphipod *Hyalella*, larval damselflies, physid snails and oligochaetes. Adults taken from streams consumed a wider range of food items than did populations in either lake or ponds, but still relied heavily (39%) on chironomids. Although of lesser importance, tipulid and simulid larvae, decapod crustaceans, mayflies, sphaeriid clams and physids were found more frequently than other food items. Fingernail clams (Sphaeriidae) formed a notable portion of the food consumed in ponds and streams, but appear to have been selected against in both situations. A predominant percentage of stomachs investigated contained some filamentous algae (181 of 282: 64%) from March through May, but this item was not considered in Table I because its true significance as a food item was not determined.

Adult feeding changed markedly with season. According to our observations, from a peak during late spring, feeding diminished with the progression of summer, increased again in early fall, and appeared to cease entirely during winter months. The stomachs of 31 fish captured from ponds during 15 December 1970 to 1 February 1971 contained no food. Wire traps used to capture these specimens were usually left unraised for 12-hour periods; however, peptic digestive rates during winter are sufficiently low (Nordlie, 1966; Baur, 1968) that some food should have remained if the fish were actively feeding. Measurable quantities of food did not appear in the stomachs until mid-March, corresponding to temperature increases above 10°C.

Larval and juvenile feeding appeared even more selective than that of the adults. Table 4 lists the food items consumed by 68 larval bullheads from Wilgreen Lake and Pond I. Since larval food analysis was not accomplished for stream populations, these data are not comparative. They did indicate, however, that food was selected far more closely according to its position in the habitat than its relative size.

TABLE 4. FOOD ITEMS OF 68 LARVAL BULLHEADS: COLUMN A= EACH ITEM AS PERCENT OF TOTAL FOOD COMPLEMENT: COLUMN B= THE AVAILABILITY OF EACH ITEM AS PERCENT OF TOTAL: AND COLUMN C= THE ELECTIVITY RATIO.

Food Organism	A	B	C
Rotifera	1.8	12.5	-0.8
Cladocera	4.8	14.3	-0.5
Copepoda			
Copepodids	6.0	3.6	0.3
Nauplii	2.2	23.1	-0.8
Ostracoda	48.0	9.0	0.7
Amphipoda	34.0	8.0	0.6
Diptera			
Chironomidae	1.4	22.0	-0.9
Annelida			
Oligochaeta	0.1	4.1	-1.0
Nematoda	0.1	3.0	-0.9
Miscellaneous	1.2	*	....

* Density not determined

In both habitats sampled, ostracods, amphipods and adult copepods made up the bulk of the diet. Pond larvae relied more heavily on copepods than their lake counterparts, apparently because of the differential abundance of ostracods and amphipods between the two areas. Nauplii, the most abundant planktonic component, and chironomid larvae, the most prevalent benthic food, were strongly selected against. In addition, selection against other benthic elements seemed to support the observation that most larval feeding was pelagic.

Larval feeding was observed on several occasions during July and August 1970 and June and July 1971. Aggregations consisted of curious admixtures of different aged individuals. Approximately 25 to 30 % of the pods observed during June 1971 consisted of yolk-sac stages (determined from capture percentages) which according to the time required to absorb the yolk, were considered two to three days younger than the others. Forming aggregations did not begin feeding immediately, but continued to wander until a visual orientation pattern was achieved. Pods observed in Wilgreen Lake were always oriented on an axis facing the shoreline. Once disturbed, the larvae broke up into less compacted masses, submerged and swam toward open water, where they regrouped on the same imaginary axis. Feeding appeared to be restricted to a limited area

about the axis of orientation, and continued at the surface during daylight hours. Larvae were always found in the few areas where aquatic vegetation and floating algal mats were most prominent. Most observed feeding was at the water surface. However, the inclusion of annelids, free-living nematodes and chironomid larvae in the stomach contents suggested that some bottom feeding also occurred.

The mean ponderal indices for adult fish sampled from each habitat during April, May and June 1971 were: ponds, (54 fish) K = 2.55, standard error 0.38; Wilgreen Lake, (23 fish) K = 3.00, standard error 0.51; streams, (32 fish) K = 2.50, standard error 0.49. The K factors were comparable for bullheads from the three habitats; a two-way analysis of variance indicated that no significant difference occurred at the 1.0 per cent level of confidence ($F = 132.50/-2.31$).

Weight-length relationships from more extensive sampling (372 specimens) throughout the study period were established. The relationship for 167 pond specimens (age groups I through VI) fit the equation: $\text{Log } W = -4.8498 + 3.1135 \text{ Log } L$; the relationship for 45 Wilgreen Lake bullheads of comparable age was $\text{Log } W = -4.1812 \text{ Log } L$; and the same relationship for 100 stream specimens was $\text{Log } W = -2.4453 + 1.9968 \text{ Log } L$. An analysis of homogeneity of slope for the three regression curves indicated significant differences in the weight-length relationship at the 1.0 per cent level ($F_s = 29.6948/F_{2,103} = 4.82$). The correlation between growth in length and weight was particularly high for ponds ($r = 0.94$) and Wilgreen Lake ($r = 0.97$), but not for streams ($r = 0.68$).

The length-weight curve illustrated in Fig. 1 represents pond, lake and stream populations and is interpolated to express the wieght at a point where length approaches zero. The curves in Fig. 2 illustrate mean

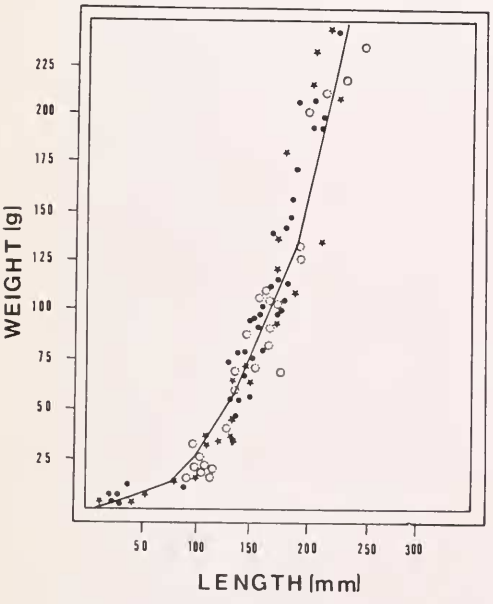

Figure 1. Length-weight relationships of 372 adult black bullheads from pond 2, Wilgreen Lake and Boone and Johnson creeks. Curve extrapolated to the point where weight approaches zero. Solid circles=ponds; solid stars=lake; open circles=streams.

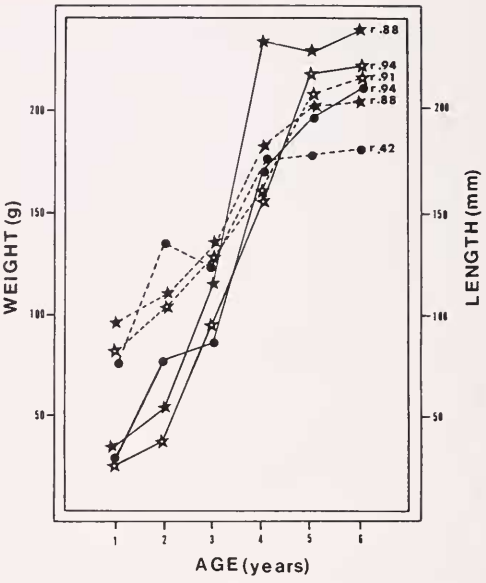

Figure 2. Mean weight and length at the time of annulus formation of 372 adult black bullheads (age groups I-IV) for ponds, lakes and streams. Each curve accompanied by a coefficient of correlation (r) computed using all measurements about the line indicated. Dashed lines=length versus age; solid lines=weight versus age; solid circles=ponds; open stars=lake; solid stars=streams.

weight and mean length (mm) as functions of age at the time of each annulus formation. Each curve is accompanied by a corresponding coefficient of correlation computed for all measurements within the range. In computing these data, July 1 was taken as the date of annulus formation (year class I), although experimental evidence indicated that most black bullheads (27 to 31 or 87 per cent) formed the annulus before the third week in June.

Correlation between growth in length, growth in weight and age in years, as indicated in Fig. 2, are quite variable among the three habitats. The most rapid growth rates were apparent in the Wilgreen Lake and stream populations, which also had the most favorable length-weight relationships and mean ponderal indices for all age groups studied. Growth in ponds was rapid to the time of second annulus formation, but showed a definite lag between the second and third year. In general, past the age of two years, pond bullheads had much lower growth rates than their counterparts in the other two habitats. No bullheads older than six years were taken during the study, and it is apparent from Fig. 2 that fish approaching the age of six already had begun to show unfavorable growth rates.

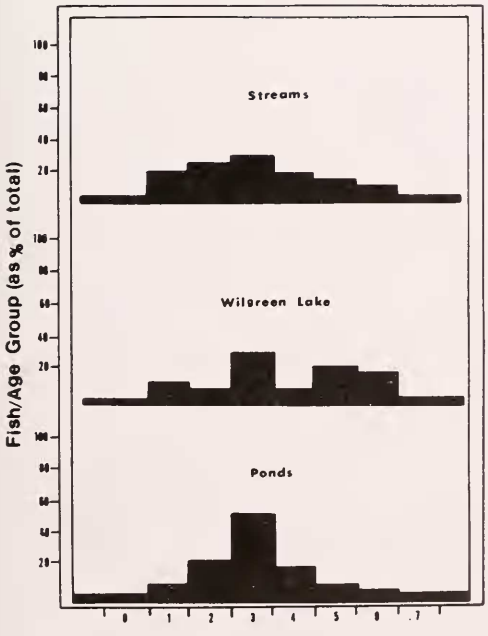

Figure 3. Age composition of pond, lake and stream populations determined from capture percentages.

Fig. 3 illustrates the population composition for the habitats sampled based on catch data. These data show definite population trends, i.e., survival through age three (the age at which most bullheads reached reproductive maturity) in ponds and streams was nearly linear, followed by an inversion of the trend after first spawnings. The polymodal nature of the Wilgreen Lake population may not represent the true population trend, but may reflect sampling bias associated with several different sampling methods, e.g., electro-fishing and trammel netting were more selective for older fish.

The populations in Ponds I and IV were subjected to mark-recovery estimations of population levels. Pond I, in conjunction with natural mortality estimates, was analyzed three times during the period October 1, 1970 to July 10, 1971. Pond IV was estimated only once, prior to the 1971 spawning season.

Pond I represented the special situation in which no fishing mortality (p) occurred during the period of investigation, but samples of the population were removed periodically. With certain carefully chosen assumptions, this situation was made to fit the Model II-B analysis of Regier (1962). The model was derived from the fact that mortality rates are either zero, infinite or directly proportional to the number of individuals in the population. Since the natural mortality (q) was assumed finite and constant, and the fishing mortality (sampling mortality in this case) was measurable over short periods of time, (q) was derivable through step-wise interation. An estimate of the natural mortality was obtained by partitioning population extremes about the calculated population line, and drawing from that line the tangent to a horizontal axis. Then, $q = -2.303\ c \tan O$, where c was a correction factor between the calculated slope b' and

the true slope be determined from linear measure of the unit cycle on the semi-logarithmic plot (Fig. 4).

The natural mortality coefficient, calculated according to the graphic method illustrated in Fig. 4, and the relationship $q = -2.303\ c \tan O$ was 0.89. Extrapolated along the line $t_0 + 1$, the population curve extends for a period of one year. Thus the coefficient 0.89 represented the probability that any fish in the population would die at any designated instant in time throughout the year. Observations carried out at Pond I indicated that black bullheads were more vulnerable during spring and early summer than during other seasons of the year. Population estimates determined on October 1, 1970 (680 individuals; 413 fish per ha) and April 15, 1971 (561 individuals; 341 fish per ha) suggested that the population remained relatively stable during winter months. During the week of 13 May 1971 a mass mortality occurred in this pond, which claimed an estimated 200 fish, or 35 per cent of the original population. A similar and coincident die-off occurred in Pond V. This mortality occurred after the calculations discussed above were performed.

Reproductive Development

The reproductive development curve for pond bullheads was examined during the 1970-71 season. Fig. 5 depicts the gonad development sequence, where points are plotted as gonad weight-body weight ratios. Although the sequence of development was not followed throughout the season for lake and stream populations, spring and summer ratios for these populations are superimposed on pond curves in Fig. 5. Five stages were apparent in the development of pond bullheads. Table 5 presents delimitation of each stage, accompanied by its significance and gross morphological appearance.

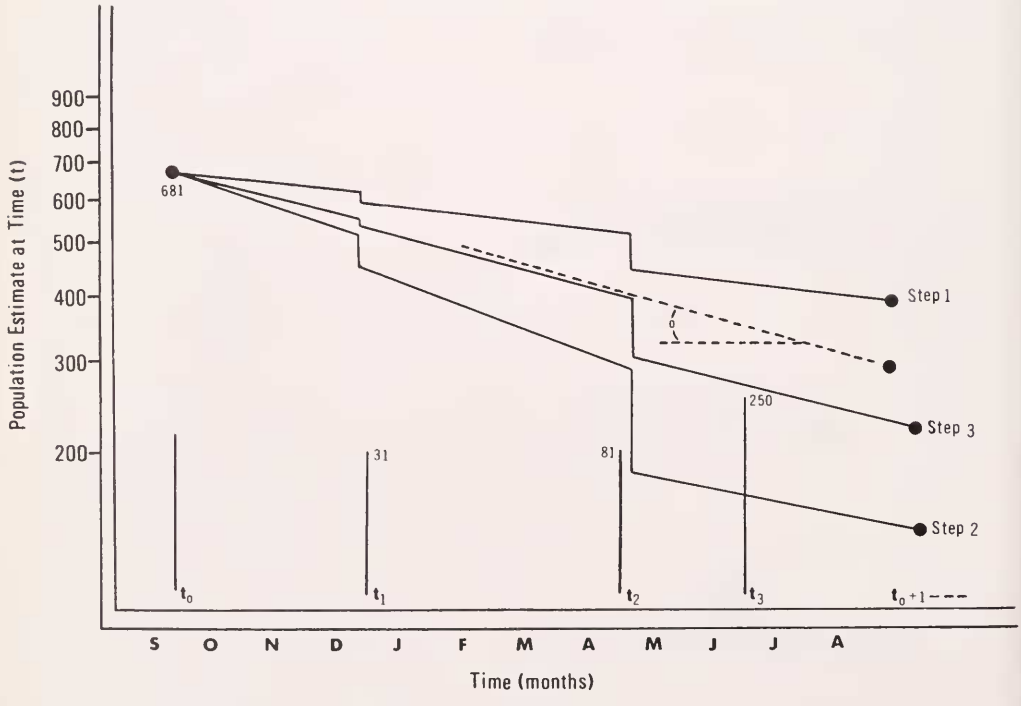

Figure 4. Graphic illustration for determination of the natural mortality coefficient (Q) by the method of stepwise iteration about the true population line.

The gonads of both males and females were at their lowest point during the post-spawning period; however, this period was apparently relatively short. Males taken during late August and early September had gonad/body weight ratios that averaged 0.7 per cent, as opposed to 1.2% for mid-August males. Female ratios varied more than those of males, but showed a corresponding increase (5.8 to 6.2%). The weight ratios of both sexes decreased sharply between September 15 and October 15, and remained low (0.3 to 0.4 for males and approximately 5.2 for females) throughout the winter. Gonad development in the spring was not an instantaneously initiated response. Although the reflex, once triggered, appears to have been irreversible, there was considerable fluctuation in the mean response with time, seemingly related to fluctuating temperatures.

Mature females reached their peak gonad development (12.1%) on 23 June, and remained relatively high until sampling was terminated on 10 July 1971. The 1970 indices remained high (10.0 to 11.5%) until mid-July. Mature males appeared to reach a reproductive peak later than females. An

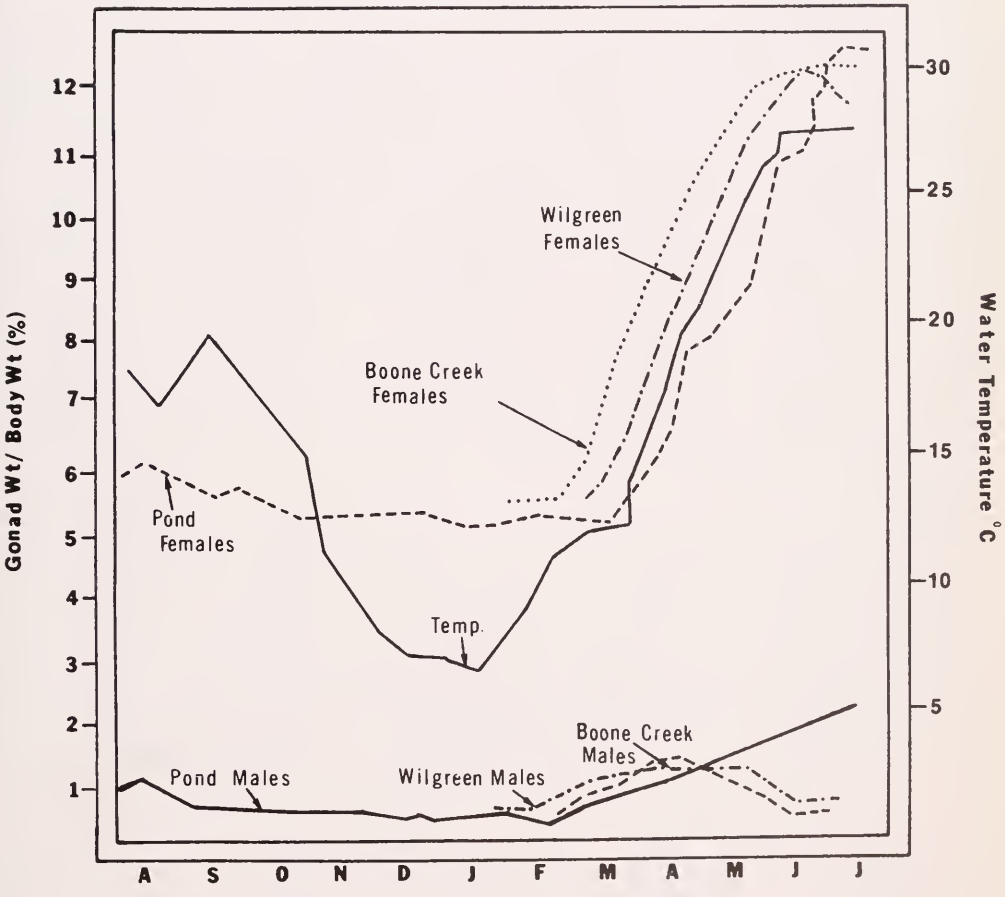

Figure 5. Gonad development curves for black bullheads obtained from ponds for the 1970-71 cycle. Imposed on the curves are corresponding records for Wilgreen Lake and Boone Creek obtained during spring and summer 1971. See Table 2 for temperature measurements.

Table 5. Appearance and significance of each stage in the gonadal development of black bullheads from pond populations.

Stage of Development	Appearance of Gonad		Significance of Stage	Period of Stage
	Male	Female		
(1)	Ribbonlike; 0.3 to 0.5 mm; extremely fimbriate margins; creamy white.	Elongate; opaque; contains primordial germ tissue and limited fat; poorly vascularized.	Quiescent stage; fat previously mobilized decreases as stage progresses. Gonad containing only primordial germ tissue.	Sept.-Feb.
(2) Developing Stage	Ribbonlike; with fimbriae increasing in dimension; pink color resulting from increased vascularization.	Oblong; eggs apparent, adhering to ovary wall; vascular areas give ovarian wall translucent appearance.	Represents initial maturation and appearance of sex products.	March-May
(3) Spawning Condition	Ribbonlike appearance lost; gonad 0.5 mm wide, 0.25 mm thick; pinkish white due to increased vascularization.	Eggs 0.5 mm in diam.; yolk fully developed and eggs free from ovarian wall; wall richly vascularized; profuse yellow color.	Sex products free in gonad (females). Both sexes ready to release sex products.	June 23 - July 1 (Females) July 1 August 1 (Males)
(4) Spent	Gonad ribbonlike as in Stage (1); uniform gray-white appearance.	Gonad flaccid; vascularization diminished to stage (2) condition; ovary wall transparent with numerous undeveloped germ cells adhering.	Sex products liberated.	Early to mid-August
(5) Recovery	Ribbonlike; gonad takes on appearance of stage (2)	Adhering germ cells fully resorbed; fatty during winter material remobilizing in gonad.	Recovery material used for maintenance.	September 1 to November 1.

TABLE 6. FECUNDITY OF BLACK BULLHEADS FROM PONDS, WILGREEN LAKE AND BOONE AND JOHNSON CREEKS. STANDARD ERROR IN MM: $S_{\bar{X}}$ = STANDARD ERROR OF ESTIMATED MEAN.

PONDS SL = 190(178-208)			WILGREEN LAKE SL = 198(186-220)			STREAMS SL = 182(164-200)		
N	Egg No.	$S_{\bar{X}}$	N	Egg No.	$S_{\bar{X}}$	N	Egg No.	$S_{\bar{X}}$
23	2552	163	7	3372	184	17	2645	237
$t_{(1,2)} = 3.3373/2.2829$			$t_{(1,3)} = .3212/2.1785$			$t_{(2,3)} = 2.4265/2.3101$		

average peak of 02.1% was recorded on 1 July 1971. Although no male samples were taken after 5 July 1971, results from the 1970 season suggested that males retain this condition for approximately 30 days.

Immature males and females had gonad development curves that mirrored those of adults throughout a good portion of the cycle. However, after reaching a plateau well below the levels found necessary for successful spawning, material previously mobilized in the gonads was rapidly reabsorbed. At the time of spawning immature gonads again reflected the refractory condition (Table 5).

The fecundity of 47 mature females of comparable size-ranges from pond, lake and stream populations was determined by a combination of displacement and egg-count methods. Table 6 presents the mean fecundity of comparable size-range females, standard errors of mean egg number estimate and Student "t" comparisons between each sample. Pond females had lower mean fecundity than females in either of the other two habitats. Analysis by Student "t" comparisons indicated significant difference between the mean fecundity value for Wilgreen Lake and the other two populations; however, the limited number of mature spawners analyzed from the former population could have masked the true relationship. Mean fecundity in ponds and streams was not significantly different ($P > .05$).

Attempts to determine egg and hatching mortality in the laboratory were unsuccessful. Subsequent to treatment with dried carp pituitary, females exhibited a sequence of behavioral changes that suggested reproductive readiness. These females went through stages of appeasement when confronted by a male, and two of the five remaining after the fifth injection constructed nests. However, males similarly treated with dried pituitary remained refractory even though long day photoperiods and temperature regulation were imposed.

On 4 July three of these pairs were terminated and their gonad/body weight ratios determined. One female (SL 207 mm, 245 g) had a ratio of 13.1 per cent, exceeding the upper limit for females taken from the wild. The remaining females (168 mm SL; 102.1 g and 172 mm SL; 134.2 g) had ratios of only 1.2 per cent and 3.24 per cent, respectively. Males ranging in standard length from 180 to 185 mm, and in weight from 132 to 139 g, had ratios of 1.5, 1.9 and 2.0, mirroring the reproductively mature condition seen in the wild (Fig. 5).

Physiological Ecology

Table 7 considers routine oxygen consumption rates for the first four free swimming stages of the life cycle of black bullheads acclimated at 7°, 12° and 23°C. Since postlarvae and juveniles were separated by

TABLE 7. ROUTINE OXYGEN CONSUMPTION RATES FOR STAGES POSTLARVA THROUGH AGE II AT 7°, 12° AND 23° C WITH THE CORRESPONDING Q_{10} VALUES BETWEEN ACCLIMATION TEMPERATURES.

Postlarva and Juveniles (A)			Yearlings (B)			Age Group II (C)		
Temp °C		oxygen consumed (ml O_2/hr)	Temp °C		oxygen consumed (ml O_2/hr)	Temp °C		oxygen consumed (ml O_2/hr)
(1) 23		0.28	23		0.17	23		0.09 (a)
	Q_{10}	1.78		Q_{10}	1.18		Q_{10}	0.12
(2) 12		0.15	12		0.14	12		0.11 (b)
				Q_{10}	1.01		Q_{10}	0.95
(3) 7		*	7		0.13	7		0.11 (c)

Significance tests (Student "t") by column and row:

Items indicated were significant at 5% level of confidence.

Column B	Row 1	Row 2	Row 3
1-3	A-C	B-C	B-C
	B-C		

* Not determined at this temperature

only a few days from the transformation date, their consumption rates were grouped. The values listed in Table 7 are accompanied by Q_{10} values computed between readings at the different acclimations. The lower portion of this table contains Student "t" comparisons for individual listings according to column and row.

These data appear to represent a uniform graded series of oxygen consumption for the life stages examined. Table 7 shows that significant differences occurred only between the extremes of observation, i.e., between postlarvae and Age II at 23°, yearlings and Age II at 23°C, and between yearlings at 12° and 23°C. The mean consumption rate for Age II at 23°C was lower than at the other acclimation temperatures; however, the means are not widely separated over the range tested, and there was no significant difference between any two readings in the series. The Q_{10} values computed between each pair of acclimations ranged from a high of 1.78 between larval means at 12° and 23°C, to a low of 0.12 between the means of Age II at these same acclimation temperatures.

Oxygen consumption increases in a nearly linear fashion when plotted on a double logarithmic grid (Fig. 6), where the lines are fitted by a least squares method. Such a plot, if representing a true linear relationship, presumably should show the magnitude of temperature effect on oxygen consumption by changes in the slopes of the lines for different temperatures. Fig. 6 reveals that there was less than an ideal lineation between the log of oxygen consumption (mg) and the log of weight in grams. However, since the tendency for consumption to decrease with respect to the log of weight after the first year was constant for the two temperatures, the slopes of the two regression lines were analyzed as to their homogeneity. There was no significant difference apparent between the slopes ($F_s = 1.0018/F(1, 38) = 7.35$).

Oxygen consumption rates were also

measured for fish ranging from 20.15 to 37 mm as functions of decreasing oxygen concentrations. It was found that these bullheads could extract maintenance oxygen down to 0.01 ml/hr in oxygen tensions of 0.2 to 0.5 ppm. Below these levels, asphyxiation was imminent, and the runs were terminated. Carbon dioxide tensions of 10.5 to 21.0 ppm were routinely determined by titration with 0.01N NaOH at the points of minimum maintenance.

Mean critical thermal maxima (CTMax) for the four age groups, postlarva through age II, are graphically illustrated in Fig. 7. Here also, physiological tolerance was related to stage of development. Postlarvae, acclimated to 12° and 23°C, had critical thermal maxima that increased 0.14°C per degree increase in acclimation temperature, in contrast to 0.09, 0.14 and 0.23 for juveniles, yearlings and age II, respectively, over the same range. There were significant differences in the effects of acclimation temperature on different age groups. All four groups had significantly different means at 23° and 12°C, ($P = 0.05$); however, only the age II group had a significant difference in the mean of 7° acclimation when compared to the two higher means ($P < 0.05$), although the spread may not have been adequate to demonstrate difference.

Temperature-preference ranges were determined for the first three age groups (above). Selected frequencies, along with

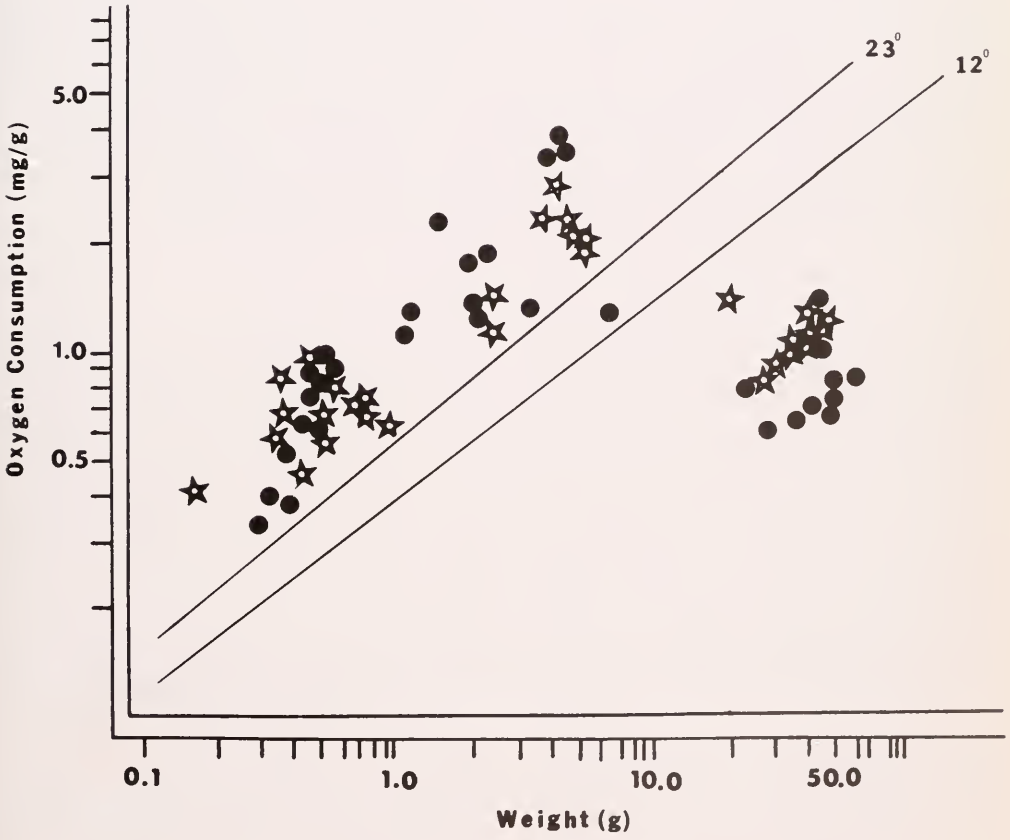

Figure 6. The influence of weight on routine oxygen consumption at 12° and 23°C. Solid circles= 23°log Y=−0.189 + 0.075 log X; open stars=12°log Y=−0.042 + 0.1124 log X.

TABLE 8. ANALYSIS OF TEMPERATURE PREFERENCE OBSERVATIONS FOR POSTLARVAL, JUVENILE AND YEARLING BLACK BULLHEADS AT 7°, 12° AND 23°C. M= MEDIAN FREQUENCY SELECTED, N= NUMBER OF ANIMALS OBSERVED, R = DURATION OF EACH OBSERVATION IN HOURS, x^2/x^2 .05 FOLLOWING EACH COLUMN COMPARES THE SELECTED FREQUENCIES OF ALL GROUPS AT THE SAME ACCLIMATED TEMPERATURE, AND x^2/x^2 .05 FOLLOWING EACH ROW COMPARES THE SELECTED FREQUENCIES OF INDIVIDUAL GROUPS AT THE THREE ACCLIMATION TEMPERATURES* . POSTLARVAE WERE NOT ACCLIMATED AT 7°C.

7°			12°			23°			
N	R	M	N	R	M	N	R	M	x^2/x^2 .05
Postlarva			Postlarvae			Postlarvae			
			10	9	25.1-27.0	10	9	23.1-25.0	17.89/3.84
Juveniles			Juveniles			Juveniles			
10	9	17.1-19.0	10	9	21.1-23.0	10	9	19.1-21.0	7.92/4.82
Yearlings			Yearlings			Yearlings			
9	9	19.1-21.0	10	9	19.1-21.0	10	9	19.1-21.0	26.02/4.82
x^2/x^2 .05		28.67/3.84			30.68/4.82			35.55/4.82	

* In order to compare the selection frequencies, the assumption was made that groups representing the same population with respect to temperature preference should have the same median frequency. After making this assumption, the frequencies were treated with the nonparametric "Median Test" of Downie and Heath (1961).

methods of comparison, are presented in Table 8. Generally, temperature preference inflected downward with progressive stage of development. In addition, acclimation to lower temperatures shifted preference temperatures upward for the first two life stages. Preference temperatures ranged from 23.5° to 27.0°C for postlarvae; 18.0° to 21.0°C for juveniles, and remained relatively unchanged with acclimation, 19.1° to 21.0°C, for yearlings. These data were gathered over nine-hour periods in continuous light. Postlarvae, brought into the laboratory from 23°C environmental temperature, showed a characteristic ascendence toward the temperature shown in Fig. 8; however, after 10 hours in the chamber these fish almost instantaneously shifted to a lower temperature (17.5° to 19.0°C). Two more sets of larvae were acquired to determined the character of this shift, and on each separate run the same phenomenon was observed.

These data, along with critical thermal maxima and lower lethal temperature points (determined as the point at which no further death occurred with time) were represented as incorporations into the over-all thermal picture. Fig. 8 displays the thermal polygons of postlarvae, juveniles and Age II. Since lower lethal temperatures were not determined for yearling bullheads, only their preference was imposed on the graph. Fig. 8 shows that each stage had a distinctly different temperature polygon. Postlarvae had the highest upper mean limits, but this increase was compensated by the upward inflection of lower limits. Larvae measured at 23° had a lower lethal temperature of 9°C, and at 12°C acclimation, a lower limit of 7°C. Juveniles acclimated at the same temperatures had lower lethal limits at 2.5° and 4.0°C, and Age II individuals had limits of

0.5° and 1.0° at 12° and 23°C, respectively. The two latter groups, when acclimated at 7°C, had lower lethal temperatures corresponding to the freezing point of water. Preliminary analysis suggested that the true lower limit was probably more closely related to the supercooling capacity of the water. Samples of blood serum, washed with heparin, centrifuged and suspended with equal volumes of water in an ethylene glycol bath suggested that serum had a freezing point of 0.8°C lower than the freezing point of water. However, this investigation was too limited to merit consideration here.

DISCUSSION

Population Dynamics

There has been disagreement in the few past studies that have sought to determine black bullhead feeding habits, although the differences may be more apparent than real since the individual authors used different terminology and were not principally interested in electivity and the relative abundance of food. Several authors (Trautman, 1957; Clay, 1962; Smith, 1949) assessed the feeding habits of this species as truly omnivorous. Forney (1955) and Viosca (1931) suggested that feeding probably was selective, since great numbers of chironomids were consumed. Rose and Moen (1951), on the other hand, contended that this tendency to rely on chironomids simply reflected the preponderance of this item in the food supply. Kutkuhn (1955) listed a variety of food items taken by adults; however, no single item was assumed to predominate in the food consumed. None of these investigations employed selective feeding analysis.

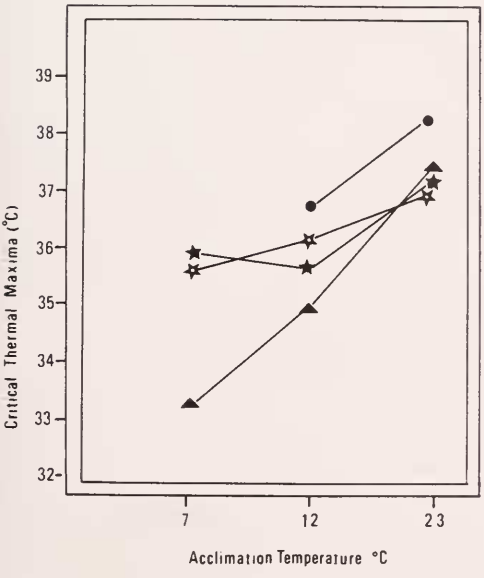

Figure 7. Mean CTMax values for stages post-larva through age II at 7°, 12° and 23°C. Post larvae were not acclimated at 7°C; consequently, only the means obtained at the other acclimation temperatures are included. Solid circles=post larvae; open stars=juveniles; solid stars=yearlings; solid triangles=age group II.

Our study clearly demonstrated that certain foods were selected for, and others against, and that although chironomid larvae and pupae did make up a sizeable percentage of the total complement (39.0 to 55.0%) in lake, pond and stream habitats, their selectivity ratio was no greater than less abundant foods (Table 3).

A notable percentage of specimens captured prior to the spawning season 1971 had eaten measurable quantities of filamentous algae and plant debris. Forney (1955) indicated that there was a necessity for this species to feed on plant material in order to reach reproductive readiness, and Raney and Webster (1940) noted a sequence of feeding in early spring which included several plant foods. We could not substantiate the former contention during this study. One of the ponds most heavily sampled during the survey contained no plant material except members of the Cyanophyta, yet the bullheads in this pond reached reproductive readiness, as expected, during the 1969-70 and 1970-71 seasons. Feeding intensity, but not pattern, changed markedly throughout the year.

Stream populations took a greater variety of food items than did individuals in either of the other two habitats. Possibly this resulted from greater availability rather than enhanced selection.

Larval feeding appeared to be even more selective than that of adults. Larvae and

juveniles relied heavily on the aquatic amphipod *Hyalella,* ostracods and adult copepods, but selected strongly against the nauplius larva of the latter and the truly benthic components relied on most heavily by adults. This was essentially the same food consumption described by Ewers (1931) and Forney (1955). However, the former authors concluded that peaks of feeding activity occurred just before dawn. Early morning samples taken during this survey indicated that relatively less feeding occurs during early morning than during mid-day. With respect to food selection, no other studies have indicated preferences as functions of available items. We concluded that items were selected for, not according to their availability, but according to the position and abundance they assume in the habitat.

Observation of larval feeding suggested that it occurred along a visually or otherwise determined orientation axis. Since it is well documented that young bullheads have poor visual acuity, and correspondingly advanced chemical perception (Bowen, 1931), orientation is believed to result from a combination of sensory mechanisms. However, orientating larvae appeared to establish an axis of the Y-axis type described by Ferguson, Landreth and Turnipseed (1965). Disturbed larvae tended always to reaggregate toward this imagined line which formed perpendicular to the shoreline. Feeding also appeared to be restricted to a rather limited locus about this same axis of orientation, with the bulk of feeding occurring during daylight hours.

Ponderal indices measured during April, May and June 1971 for specimens from pond, lake and stream populations were highly comparable from one habitat to another ($P = 0.05$). Since these ratios, reported throughout the range, are quite variable from one state to the next, there seems little value in making such comparisons here (see Carlander, 1968). Comparability from one habitat to another is, however, important. Length-weight regressions for the same populations were found to be heterogeneously distributed, as indicated by analysis of their slopes ($F_S = 29.69/F(2, 103 = 4.82)$. In addition, length-weight correlations for the three populations were quite variable, the highest values obtaining in Wilgreen Lake ($r = 0.68$). It was difficult to attach significance to this finding since variance between the separate populations could lead to lower values. Investigators in other parts of the black bullhead's range have reported both high and low length-weight relationships (Dennison, 1970; Lewis, 1949; Carlander, 1968). Our findings did serve to point out that members of the single species tend to show deviate population trends when encountered in different habitats.

The size in length and weight at the time of annulus formations were compared. Generally, increase in length was more closely related to age than increase in weight (Fig. 2). The size at the time of each annulus formation showed greater mean differences in ponds where there was a growth lag between the second and third year. This finding is in line with the conclusion drawn by Houser and Collins (1962), who found that growth rates in Oklahoma bullhead populations were lowest in ponds. It also appears to augment the observations of Moen (1959) that black bullhead growth is retarded according to the degree of intraspecific competition, which is doubtlessly more influential in ponds than in streams. Three of the ponds utilized during this study, Ponds I, IV and V, were overcrowded with bullheads. A fourth pond, Pond II, was overpopulated by the bluegill sunfish. However, the effect of overcrowding by this second species was not reflected in bullhead condition. Population estimates in Pond I indicated the conditional and genetic effects of crowding. On October 1, the population of this pond was estimated at 681 fish, or 1,021 fish per surface acre of water (431/ha). Hastings and Cross (1962) and Fredin (1950) reported the presence of similar sized populations in turbid ponds, and commented on the relationship of crowding to weight gain. The age-weight correlation determined for ponds during this study (heavily weighted by crowded pond specimens) was quite low ($r = 0.42$).

A great number of abnormalities were observed in the Pond I population, apparent-

ly resulting from overcrowding. Several fish were captured which lacked one or more fins, and one individual captured during July 1971 had no paired fins at all. In addition to abnormal fish, most of the breeding population in this pond suffered from bacterial fin rot during spring and early summer. Microscopic examination revealed the presence of a proliferative streptococcus bacterium.

Apparently, then, from samplings of three different populations within a comparable area, the greatest population success is probably achieved in ponds, as indicated previously by Houser and Collins (1962). However, this does not imply that greatest population survival also occurs in ponds. From observations during the period September 1, 1970 to July 10, 1971 a natural mortality

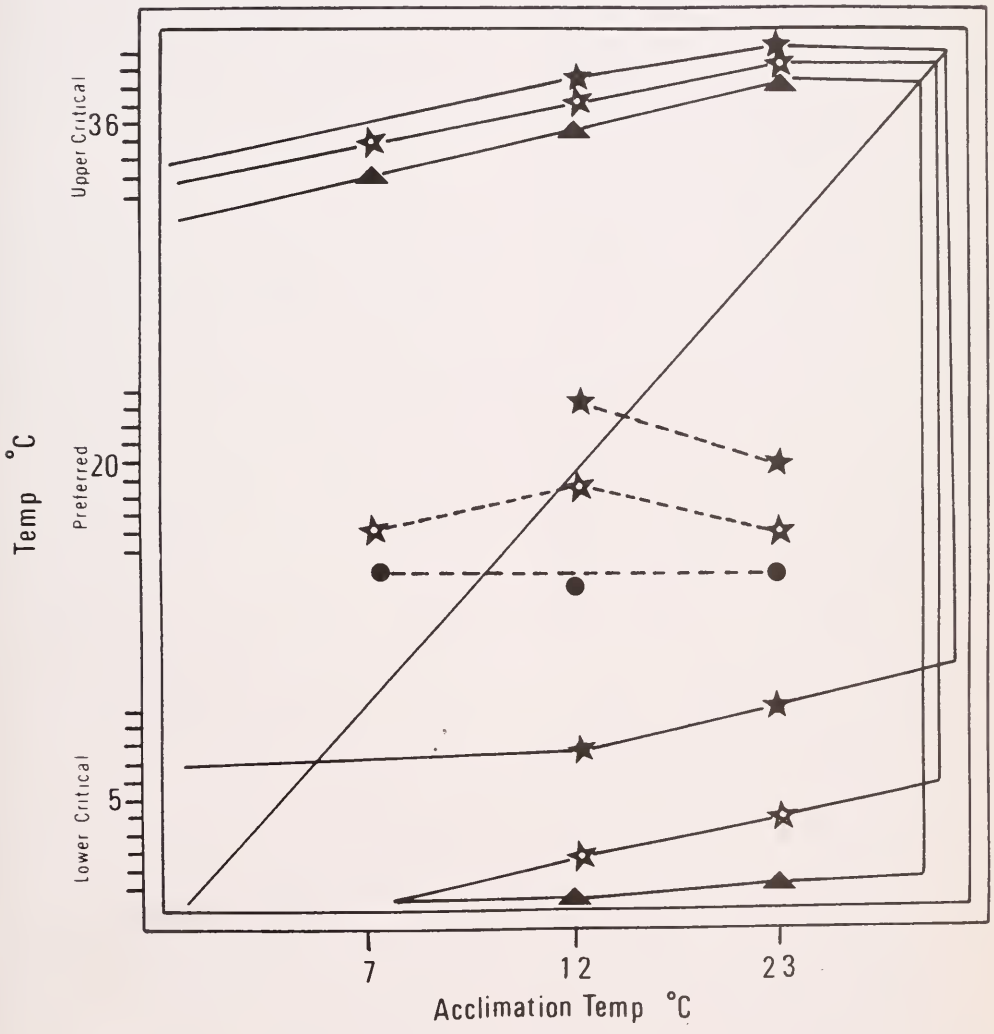

Figure 8. Relation between mean upper and lower lethal temperature limits expressed as functions of acclimation temperature for stages postlarva, juvenile and age II. Included are the preferred temperatures of postlarvae, juveniles and yearlings similarly expressed as functions of prior acclimation. Solid stars= postlarvae; open stars=juveniles; solid circles=yearlings; solid triangles=age group II.

coefficient was computed for the population of Pond I. The result suggested that each adult fish in the population had only an 11 per cent chance for survival throughout the year. Apparently, there are no natural mortality estimates available with which to compare this one. Taken as an absolute value, however, it does indicate that mortality was high for the period of one year. However, further estimates of population sizes suggested that mortality was neither infinite, nor evenly distributed throughout the year. A population estimate made during the week of 15 April 1971 disclosed the presence of 562 bullheads, 83% of the original estimate that had survived through the winter. Thus, heavy mortality did not occur during winter months. This seems to augment the contention of Forbes and Richardson (1908) that black bullheads enter a relatively quiescent state during periods of prolonged cold. Nordlie (1966) further noted that peptic digestive rates could be directly related to temperature regimens, increasing or decreasing with temperature over relatively short periods of time. Fish were captured throughout the winter, and on one occasion the ice was broken in order to remove traps containing bullheads. These fish had no food in their stomachs, but were active enough to enter traps. Thus, although retaining some active impulses, winter bullheads appeared to survive reasonably well without food by the conformity of certain physiological mechanisms to reduced temperatures.

During the second week in May 1971 a naturally occurring mass-mortality was observed in Ponds I and V. This occurred during a period of heavy rainfall and unseasonally cool weather, and the water temperature in Pond I was reduced 7.0°C. Although the overall water chemistry picture did not change appreciably, the dissolved CO_2 concentration increased from 4.5 to 14.0 ppm over a two-day period (Table 2). An estimated 200 fish died in Pond I, 29% of the original population estimate. The bulk of the mortalities were older fish, and mature individuals approaching the breeding condition. Powers (1937) commented on similar mortalities and implicated CO_2 changes as the most instrumental factor in mortality. This contention, however, could not be substantiated during our investigation.

Black bullheads older than six years were not taken during this study. This seemed to indicate that the longevity for members of the species was relatively short, and in Fig. 2 one sees that bullheads approaching the age of six had already begun to show unfavorable incremental growth. Rose and Moen (1951) followed a single black bullhead year class through 10 consecutive years in Lost Island Lake, Iowa. Few individuals survived past the age of seven, and those that did remain showed unfavorable growth rates.

Reproductive Potential

As noted in Table 5, material began mobilizing in the gonads of pond bullheads shortly after the spawning season; however, most of this extragonadal tissue had been reabsorbed before temperature increases in spring initiated the developmental stage. From the quiescent stage brought on by cold it could be surmised that this same sequence should prevail in all populations. However, stream bullheads spawned at least one month previous to the other populations, with peak gonad/body weight ratios attaining during early and mid-May (Fig. 5). Two apparent explanations might account for this difference in spawning time and developmental sequence: (1) although constant rise in temperature appeared to initiate the reflex in ponds (Fig. 5), and in lakes (Dennison, 1970), a separate and distinct set of conditions might prevail to initiate the spawning response in streams; (2) as Aronson (1955) disclosed for the cichlid *Tilapia heudiloti*, which spawns throughout the year but has spawning peaks corresponding to the vernal and autumnal equinox, each individual may have a temperature threshold distinct from others in the populations, producing noticeable differences when different habitats are considered.

Pond and lake spawners also react differently to temperature. Dennison (1970) indicated that once initiated the response in Clear Lake, Iowa, was nearly linear and un-

interrupted. In both situations, once initiated, the developmental sequence appeared to be irreversible. In Wilgreen Lake, where temperature fluctuations were not marked over short periods of time, the gonad/body weight curves showed interrrupted increases. In contrast, corresponding ratios for pond spawners fluctuated directly with temperature change (see Table 2). This probably was a parametric manifestation of the alternate speeding-up and slowing-down of physiological rate functions in response to rather widely fluctuating temperatures (Table 2). Regardless of the influence, pond spawning lagged behind that of Wilgreen Lake, with pond males and females reaching the most favorable gonad/body weight ratios (2.1 and 12.1%) on July 3 and June 23, respectively.

The above comparison shows that the habitat imposed its own limit on breeding time and the sequence of reproductive development. Thus, it is not difficult to reckon if one considers that different bodies of water mediate environmental modifiers differently and prompt the establishment of genetic stocks that adjust the breeding sequence to the most favorable period of the year.

Fecundity determined during this study also showed considerable variability when all three habitats were considered. Greatest mean fecundity per individual attained in Wilgreen Lake (mean = 3,372), with ponds exhibiting the lowest value (mean = 2,552), and streams intermediate (mean = 2,645) (Table 6). Mean values between the lake and other populations were significantly different at the 5% level of confidence.

Few fecundity estimates have been published for black bullhead populations and the reports that have appeared have represented lake populations. Thus, the data obtained during this study probably are more significant when the different habitats are compared. Pond fecundity apparently is reduced coincident with the limits of intraspecific competition, similar to the situation that accrues with growth (Moen, 1959). This assumption is difficult to make for streams which had equally low mean fecundity. Data for Johnson and Boone creeks were combined to arrive at the value listed in Table 6; however, from individual estimates made in Boone Creek during the 1969-70 season (7 specimens) we assumed that all overall fecundity was greater for this stream (mean = 3,845) than for the other. Johnson Creek presented a situation similar to that observed in ponds. The water was turbid during the period of sampling, and on a single night of seining over 500 bullheads were hauled from a .20 km section. Therefore, overpopulation here seems to have had an effect on mean fecundity similar to that recognized in turbid ponds.

Attempts to induce spawning in black bullheads proved unsuccessful. There has been considerable controversy over methodology when employing pituitaries to induce spawning. Early investigators (Hasler, Meyer, and Field, 1939; Pickford and Atz, 1957) insisted that only fresh preparations should be used. Indian biologists, however, have achieved considerable success with dried pituitary preparations administered through intramuscular injection (Alikuhni, Sukumaran and Parameswaran, 1962; Alikhuni and Sukumaran, 1962). The Indians indicated that great numbers of the silver carp *(Hypothalmichthys molitrix)* had to be obtained to acquire a relatively few fish that could be artificially stimulated. Others (Sneed and Clemens, 1960) preferred the intraperitoneal route of injection, but concluded that greater dosage rates are required.

Wallace (1967) used the methods detailed by Sneed and Clemens *(loc. cit.)* and was successful in inducing black bullheads to spawn; however, his results were based on the observation of a single breeding pair retained in a 400 gallon (1514 l) gallon aquarium from the end of one spawning period to the beginning of the next. Perhaps in contrast to the refractory nature of spawners held in aquaria during this study, that a pair of fish kept over an extended period may retain an endogenously controlled reproductive rhythm, such as that described for certain small mammals and birds (Pengelley and Asmundson, 1971). If so, such fish could conceivably spawn naturally.

The method used during the present study followed that of Sneed and Clemens

(loc. cit.) and Wallace *(loc. cit.)*. This method, which suggests the administration of 4 mg/lb (1.82 mg/kg) per day of dried pituitary, was devised for channel catfish, the authors suggesting that breeders should be obtained as close to the spawning season as possible. Other authors (Pickford and Atz, 1957) suggested different stages of reproductive readiness during which riverine fishes should be obtained in order to obtain the best results. Although our experimental fishes oozed gametes when strong pressure was applied to the abdomen, they did not respond to pituitary treatment. We have no explanation for the failure of black bullheads to spawn in aquaria. When our experiments were terminated on July 5, the catfish exhibited gonad/body weight ratios similar to those observed in the wild. This would seem to indicate that the attainment of reproductive readiness was not the chief limiting factor.

Physiological Ecology

Several investigators have commented on the black bullhead's ability to persist in situations that are limiting to most other fishes (Black, 1955, 1959; Lewis, 1949,; Trautman, 1957; Bennett, 1948), because of combined behavioral and physiological adaptations which enhance the ability of rate functions to remain relatively constant over a wide spectrum of environmental gradients. However, information is conspicuously meager in the area of black bullhead physiological ecology. Temperature thresholds and oxygen consumption rates have been determined in the brown (Brett, 1944) and the yellow bullheads (Morris, 1965), but only incidental treatments have been reported for the black bullhead. As indicated by Brett (1971), temperature is probably the most important controlling factor in distribution and life styles of most fish species. For this reason, tolerance points relative to different acclimation temperatures must be established, and extrapolated from them to obtain the thermal survival picture. However, Brett (1959) and Hart (1952) questioned the imposition of temperature tolerance points that fail to reflect environmental survival, i.e., the physiological and ecological limits are often widely separated. Furthermore, fishes rarely live in conditions close to their survival thresholds.

In general, temperature tolerance polygons occur as a graded series when more than one stage in the life cycle is considered (Fig. 8). Extremely high upper limits (39°C for postlarvae acclimated at 23°C), and lower limits restricted to a narrow range about the freezing point of water for older animals, assure this species a position in most habitats. We observed as well that the critical thermal maxima curves for four different life stages were also graded, each stage exhibiting a relatively flattened curve with respect to closely related species (Brett, 1956). The oldest group tested (age II), and two intermediate stages, exhibited relatively good compensatory ability with respect to temperature change; whereas postlarvae at the two acclimations 12° and 23°C showed less ability to compensate for temperature change through alteration in rate functions. Since the postlarval stage could not be acclimated to 7°C, we suggest that black bullheads are not hatched with the ability to compensate for wide change in temperature. However, since they are born during a period of the year when environmental temperatures are highest, the tolerance to high temperatures (Fig. 7) probably is most important. As indicated by the curve for juveniles (Fig. 7), after attaining a few days of age (10 to 15 days) the biochemical structure is sufficiently enhanced to permit compensations over a wider temperature range.

Brett (1956) constructed thermal polygons similar to the ones we depict in Fig. 8 for the brown bullhead. The black bullhead, as determined by us, appears to have a greater tolerance range at comparable acclimation temperatures.

Hart *(loc. cit.)* and Brett (1959) concluded that temperature tolerance is not of direct ecological significance, since fishes rarely confront such temperatures. However, our work indicates that black bullheads can or do live close to their thermal limits during at least a portion of summer and early fall. The temperature of Ponds III and IV reached 33°C even in the deepest parts on

several days during August and September. Even if temperature tolerance fails to reflect a true ecological condition, it does indicate the ability of a species to alter rate functions in connection with temperature changes, which suggests that such species function effectively over very broad thermal zones.

The temperature preferences of three age groups of black bullheads were investigated (Fig. 1). Different stages in the life cycle were found to have significantly different preference ranges over the acclimations indicated above ($P < .05$, Table 8). In addition, a phenomenon was observed in larvae which suggested the influence of temperature on life style at this stage. Postlarval bullheads held in the selection chamber for nine-hour periods behaved much like older fish. However, after ten hours in the chamber, they suddenly shifted from one preferred temperature to a lower one (from 23.5° to 17.5-19°C at 23°C acclimation). After subsequent experimental runs demonstrated the same response, we theorized that this was an environmental artifact, i.e., that larvae apparently had free running rhythms of activity. After spending daylight hours near the water surface they sought lower strata of water where seclusion was more nearly assured. We suspect that the response observed in the chamber was the same as that which occurred in the wild. Larvae apparently sought water in which to remain secluded by seeking water temperatures associated with that stratum. The reciprocal explanation could also be advanced according to the time of day.

Three levels of oxygen consumption have been described for fish: standard, routine, and active (Fry, 1968). Routine rates, which may be defined as the oxygen consumed by a fish whose only movements are spontaneous (Beamish and Mookerjii, 1964). Such readings are most frequently recorded, and their values fall between the extremes of active and standard metabolism. The rates of oxygen consumption at different acclimation temperatures are still another, and perhaps better, indicator of change in rate-function with time.

Morris (1965) stated that brown bullheads, when moved to 27° from 12°C acclimation, compensated by lowering metabolic levels from 0.35 to 0.15 ml O_2/g/hr. The routine rates measured during the present study indicated that black bullheads do not display such compensatory shifts over a 16°C change in temperature. However, since their rates were significantly low even at the highest acclimation temperature (Table 7), and since all rates were measured at 20°C, such radical compensatory shifts were not anticipated. We believe that the black bullhead is able to survive in extremes of temperature by having a relatively flattened metabolic rate curve, which hardly doubles for each 18°F increase in temperature as indicated by McCay (1925).

Beamish and Mookerjii (1964) and Basu (1959) suggested that oxygen consumption increased linearly with weight when plotted on a double logarithmic grid. This appeared to hold for our first two groups (Table 5) but not for age II individuals, whose absolute consumption fell below the best fit line (Fig. 6). However, since we assumed that the effect was constant from one acclimation temperature to another, the only factor operating to account for changes in consumption is temperature. From an analysis of the homogeneity of the slopes plotted for 12° and 23°C acclimation, we determined that there is no significant change in routine consumption for an eleven degree change in temperature ($F_S = 1.0018/F.99\ (1, 38) = 7.35$).

According to Prosser and Brown (1962) chemical reaction rates usually are more than doubled for each 10°C increase in temperature. Thus, Q_{10} values of less than 2 would indicate a relatively insensitivity to temperature. The Q_{10} values determined for black bullheads (Table 7) ranged from 1.78 for postlarvae to a low of 0.12 for age group II.

The most important observation drawn from metabolic-rate determinations was the fact that black bullhead rates decreased to a maintenance level of 0.01 ml O_2/g/hr at 0.2 to 0.5 ppm dissolved oxygen before showing signs of asphyxial stress. However, this should not be considered unique. Larimore

(1957) reported similar low levels for the warmouth, *Chaenobryttus gulosus,* and Powers (1938) found that other fishes, such as the smallmouth bass, *Micropterus dolomieui,* could extract oxygen to 0.3 - 0.4 ml/l. We doubt, however, that this fish could have established maintenance levels as low as that determined for the black bullhead.

The black bullhead is known to survive in habitats that present far less than the ideal conditions of temperature and dissolved oxygen. Presumably this is possible through a combination of ecological and physiological adaptations. The ability to subsist on a variety of foods, or on a very limited food supply, and the ability to become quiescent during periods of prolonged temperature decrease are significant adaptations to life in some of the habitats occupied. In addition, comparatively favorable high and low lethal temperature ranges, assure the species a position in most situations that might prove limiting to less favored species. Low metabolic rate-temperature curves imply at least one rate function that changes minimally with temperature, and the ability to extract maintenance oxygen in the presence of low ambient levels favor survival in most extreme situations.

SUMMARY AND CONCLUSIONS

Although the black bullhead is widely distributed in the United States it has not been studied extensively. Our study was designed to facilitate a better understanding of the species' life history and physiological responses in pond populations, as compared to other known habitats. Conclusions from data derived during April 1970 through July 1971 are summarized as follows:

1. Adult black bullheads subsist on a variety of foods, but exhibit feeding selectivity in ponds, lakes and streams. Chironomid larvae, comprising a predominant portion of the adult diet, are not more strongly selected for than other less available foods.
2. Larval feeding occurs in a rather restricted locus about an axis of visual orientation. Foods taken most frequently by young are the aquatic amphipod *Hyalella,* ostracods and adult copepods. Larval feeding was found to be highly selective.
3. Mean ponderal indices for pond, lake and stream populations do not differ significantly ($P < .05$). However, log-transformations of length-weight relationships have slopes for which the hypothesis $B = 0$ does not hold at the 99% level of confidence. Most favorable growth rates occurred in Wilgreen Lake, and least favorable in ponds. The age-weight correlation for pond populations was quite low ($r = 0.42$).
4. Populations attained high levels in ponds [1,021 fish per surface acre (= 413/ha) in one 0.65 (= .26 ha) acre = impoundment]. The effect of crowding was significantly reflected in population condition, number of genetic abnormalities and lowered mean fecundity. Also apparently correlated with high population levels was a high mortality coefficient (0.89 for Pond I of this study).
5. Mortality is appreciably higher during some portions of the year than others. Greatest mortality occurred in Pond I during spring and early summer. Population estimates indicate that mortality is relatively low during the winter.
6. Gonadal development and attainment of spawning condition in ponds lag behind that of lakes and streams. Most favorable gonad/body weight ratios occur in June for mature females (12.1 per cent) and July for mature males (0.21 per cent). In contrast, stream spawners reach development peaks during mid-May, and Wilgreen Lake spawners attain the most favorable index during mid-June.
7. Fecundity for females ranging from 164 to 220 mm SL is lowest in ponds (mean - 2,552), highest in Wilgreen Lake (mean = 3,372) and intermediate for combined samples from creeks (mean = 2,645).

8. Mature bullheads brought into the laboratory during the month of May could not be induced to spawn even after repeated treatment with dried carp pituitary gland. The gonad/body weight ratios of these fish on the termination date, 5 July, were similar to levels observed in wild populations.
9. Temperature tolerances were sufficiently high and low that few habitats could be considered restrictive to bullhead survival on the basis of temperature alone. The CTMax of age groups postlarva through Age II ranged from 36.5° to 38.2° at 23°C acclimation. CTMax curves over a temperature range of 16°C were relatively flattened, suggesting little rate-function change with temperature. Lower lethal temperature graduated upward for each descending stage of the life cycle. Preference ranges for the first three life stages were significantly different from one another at the 5% level of confidence.
10. Metabolic rate-temperatures curves, Q_{10} values, and absolute consumption at different temperatures suggest that metabolic rates change very little over a 16°C acclimation range. Black bullheads of 20.15 to 37.00 g reached the maintenance oxygen level at 0.1 ml O_2/g/hr in 0.2 to 0.5 ppm ambient oxygen.

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